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Acacia Special Issue

***Acacia penninervis* Sieber ex DC., *Prodr.* 2: 452 (1825)**
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Marion Simmons, *Acacias of Australia* (1981)

Acacia is now predominantly an Australian genus, with *A. penninervis* as the newly designated type species. It was chosen because it is the type of subg. *Phyllodineae* (the name upon which *Racosperma* was based). Like *A. penninervis*, most Australian species have phyllodes rather than compound leaves.

Editors: D. Murphy and T. Lebel

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Acacia 2006: Knowing and growing Australian wattles

a235988

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Introduction

This volume of *Muelleria* marks the introduction of a new format for the journal and is a special issue, the result of the '*Acacia* 2006' conference held in Melbourne from 26 to 28 August 2006. Titled 'Knowing and growing Australian wattles,' the conference was jointly hosted by the Royal Botanic Gardens Melbourne and the Australian Plants Society Victoria as part of the biennial F.J.C. Rogers seminar series. These papers provide a valuable snapshot of the large genus *Acacia s.s.*, so important in Australia, and extensively utilised internationally. Most authors in this issue have provided review-style papers, reflecting their different areas of expertise. The review nature of the papers was seen to be necessary to contextualise, for a general audience, some of the work that is being undertaken on *Acacia* and for this reason we have broadened the scope of *Muelleria* beyond systematics, taxonomic revisions, nomenclature matters, and phylogenetic and biogeographical studies, to include these papers. The entire program of talks at the '*Acacia* 2006' conference can be found in Murphy (2006) and the horticultural proceedings volume (Australian Plants Society Inc, Maroondah Group 2006).

The diversity of *Acacia s.s.* in Australia is astounding, some of which is illustrated in Figure 1. The genus (in the strict sense) comprises almost 1000 species, and is confined to the Australian continent except for a few species found on islands from Hawaii in the Pacific Ocean to Madagascar in the Indian Ocean. The range of topics covered in this volume reflects this diversity as well as the variety of research interests in the genus.

But first, due to recent name changes to *Acacia s.l.*, it is necessary to make a note about the names used in this volume. Most contributors have decided to use the names of the segregate genera that follows from the retypification of *Acacia* with an Australian type (as outlined by Maslin in this volume): *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*), *Vachellia* (formerly *Acacia* subgenus *Acacia*), *Senegalia*, *Acaciella* and *Mariousousa*. For further information concerning the generic status of *Acacia s.l.*, and to keep abreast of future name changes concerning members of this group, the reader is referred to the "species

continued page 6

Figure 1. Same marphalagical diversity of *Acacia* in Australia and their sectianal placement using the classificatian af Pedley (1978). Clockwise from top left. *Acacio adaxa* var. *adaxa*, sect. *Lycapadiifolioe* (DM); *A. colei* var. *calei*, sect. *Juliflaroe* (DM); *A. pulchello*, sect. *Pulchellae* (GB); *A. tetraganacorpo*, sect. *Alatae* (GB); *A. ampliceps*, sect. *Phylladineae* (DM); *A. cuspidifolio* sect. *Phyllodineoe* (DM); *A. spathulifalia*, sect. *Phylladineae* (DM); *A. dictyophleba*, sect. *Phylladineae* (DM). Photographs by Daniel Murphy (DM) and Gillian Brawn (GB).

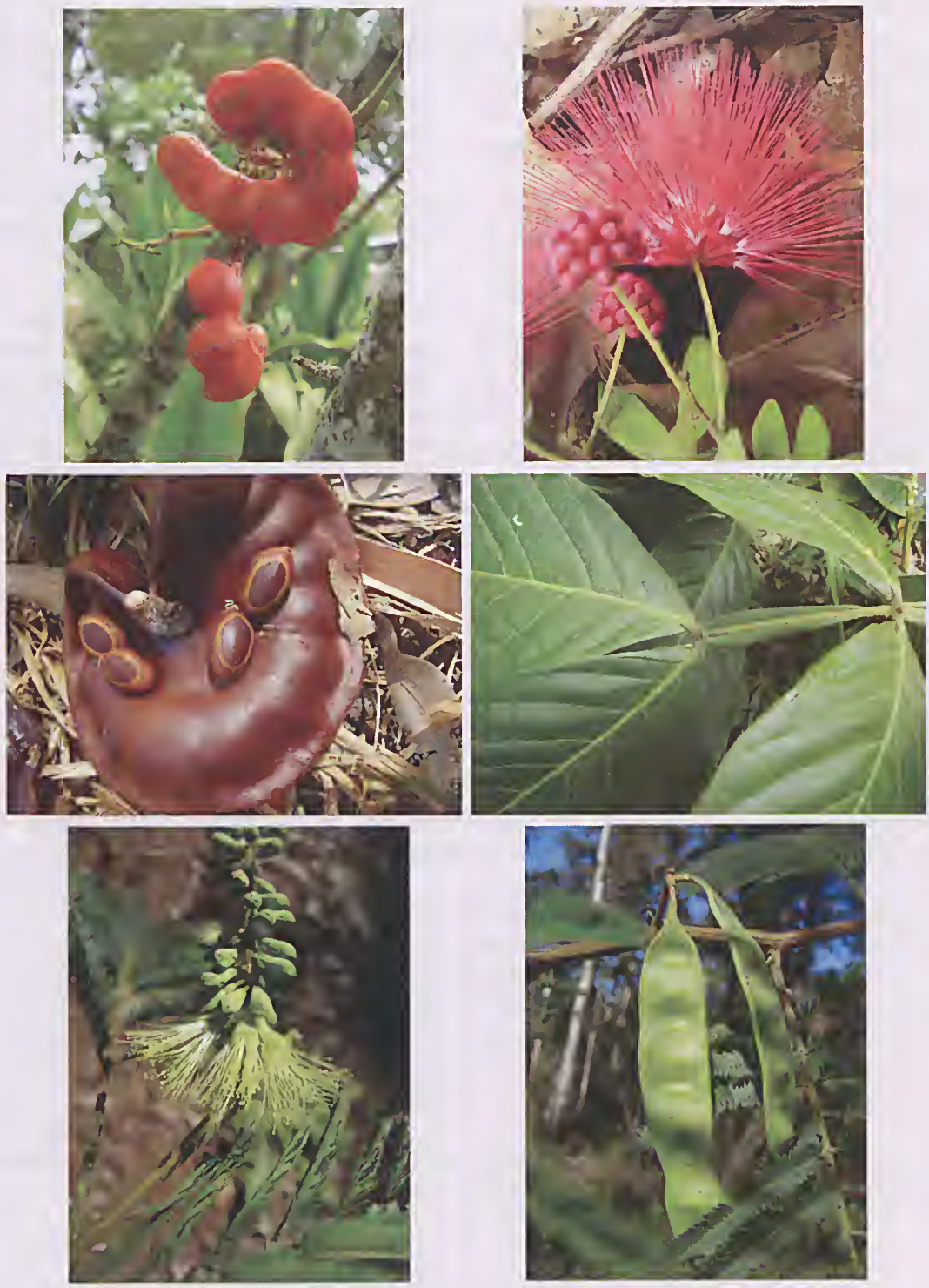

Figure 2. Pod, flower and vegetative characteristics of some members of tribe Ingeae. Clockwise from top left. *Archidendron lucyi*; *Calliandra haematacephala*; *Inga edulis*; *Paraserianthes laphantha* subsp. *laphantha* in fruit (right) and flower (left); *Enterolabium cyclocarpum*. Photographs by Gillian Brown.

from page 3

gallery" page of the WorldWideWattle website (www.worldwidewattle.com). In a very useful contribution, Maslin has provided a clear and concise summary of the current nomenclature for *Acacia s.l.*. This has previously been confusing for many people and this paper is a welcome contribution.

In the midst of the nomenclatural debate concerning the application of the name *Acacia*, it is important to remember the scientific reasons for the fragmentation of *Acacia s.l.* Murphy (pp. 10-26) reviews the historical classification of *Acacia*, illustrating the numerous studies that have shown *Acacia s.l.* is not monophyletic. Murphy then focuses on the phylogenetic studies of *Acacia s.s.* which will eventually overturn the current classification of *Acacia s.s.* and greatly enhance the evolutionary understanding of this amazingly diverse monophyletic lineage. Molyneux and Forrester (pp. 51-56) continue the systematics and taxonomy theme by describing three new and very rare species of *Acacia* from East Gippsland in Victoria.

Brown (pp. 27-42) provides a comprehensive review of the taxonomy and phylogeny of the mimosoid legume tribe Ingeae which is relatively poorly known. This morphologically diverse group is well illustrated in Figure 2. The tribe Ingeae is now known to include the closest relatives of *Acacia s.s.* and is therefore of critical importance in understanding the evolution and biogeography of the Australian *Acacia* flora. One such evolutionary insight that can be assessed in the light of its phylogeny is the classical morphological interpretation of the *Acacia* phyllode in comparison to bipinnate compound leaves, which is reviewed by Gardner *et al.* (pp. 43-50). They reassess the developmental homology of the phyllode and discuss this in the context of recent understandings in developmental genetics.

The traits of *Acacia* species that make them so successful in the Australian landscape may also predispose some species to weediness and two papers discuss some of the issues this raises in the Australian context. Adair (pp. 67-78) looks at some Australian species that have become naturalised outside their original ranges within Australia and the potential for biological control. Reid and Murphy (pp. S7-66) discuss methods for assessing whether species are naturalised or indigenous to an area using herbarium records and other evidence, and examine three *Acacia* species found on the coast in western Victoria as case studies.

The paper by Rinaudo and Cunningham (pp. 79-85) reviews the use of several Australian *Acacia* species in Africa as multi-purpose agro-forestry trees and the issues surrounding their adoption by African farmers. The importance of their work, which has the potential to assist millions of people in Africa, cannot be overstated. Along a related line of research Singhal *et al.* have undertaken a comprehensive study of the highly variable species *Acacia* ('Vachellia') *nilotica*. This species is put to many uses in India, and Singhal *et al.* (pp. 86-94) examine three varieties of *A. nilotica* to evaluate their useful traits and identify which variety is the one most suited to particular industry.

Acknowledgments

I wish to thank Rob Cross and Gillian Brown, my co-organisers of the "*Acacia* 2006" conference Scientific Program, and the Australian Plants Society Victoria Maroondah Group for the initial idea for the *Acacia* conference and for organising the Horticultural Program and associated field trips.

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Generic and subgeneric names in *Acacia* following retypification of the genus

a235989

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Introduction

There are implications for generic and subgeneric nomenclature within *Acacia sens. lat.* following the decision of the Nomenclature Session of the 17th International Botanical Congress (IBC) in Vienna to endorse the recommendation of both the Committee for Spermatophyta and the General Committee of IAPT to accept the Orchard & Maslin (2003) proposal to retypify *Acacia* Mill. with a new type. A summary of the actions of the Nomenclatural Section, including the *Acacia* decision, was presented by McNeill (2006). As a result of the IBC decision the type of *Acacia* changes from the African/Asian species, *A. scorpioides* (L.) W.F. Wright (=*A. nilotica* (L.) Delile), to the Australian species, *A. penninervis* DC. Consequently, there are nomenclatural implications at both the generic and infrageneric levels, depending upon the classification that one adopts for this large, cosmopolitan genus. As discussed by Maslin *et al.* (2003) there exists a strong body of evidence to suggest that *Acacia sens. lat.* should be divided into at least five genera (see Table 1) and although the fragmentation has commenced, not everyone has adopted this classification.

The nomenclatural consequences at the subgeneric level that flow from the IBC decision are: (1) the name subgenus *Acacia* now applies to the 'Australian group' formerly known as *Acacia* subgenus *Phyllodineae* and (2) the former *Acacia* subgenus *Acacia* requires a new subgeneric name. When *Acacia sens. lat.* is treated as comprising multiple genera: (1) the name *Acacia* applies to the 'Australian group' and *Racosperma* is a synonym of it, and (2) *Vachellia* is the correct generic name for species included in the former *Acacia* subgenus *Acacia*.

To date new combinations in *Vachellia* Wight & Arn. have been made for both the American and Australian species (see Seigler & Ebinger 2005 and Kodela & Wilson 2006 respectively). Also, in the Americas new combinations in *Senegalia* Rafinesque have been made for most of the species included in *Acacia* subg. *Aculeiferum* Vassal (Seigler *et al.* 2006; Glass & Seigler 2006), a new genus, *Mariosousa* Seigler & Ebinger, has recently been published to accommodate species of the *'Acacia coulteri* group' (Seigler *et al.* 2006), and the genus *Acaciella* Britton & Rose has been resurrected to accommodate the species in *Acacia* subg.

Abstract

This paper reviews the current nomenclature for *Acacia s.l.* in light of the decision to retypify *Acacia* Mill. with a new type. The nomenclatural implications for classifications treating *Acacia* as a single genus, or as multiple genera, are summarised.

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Aculeiferum section *Filicinae* (Benth.) Taub. (Rico Arce & Bachman 2006). However, new combinations for the African and Asian species currently included in *Acacia* subg. *Aculeiferum* and the former *Acacia* subg. *Acacia* have not yet been made.

As things currently stand, the situation with respect to both the classification and nomenclature of *Acacia sens. lat.* is rather unsatisfactory. Firstly, it is not known if or when the international botanical community as a whole will accept the split of *Acacia*, despite the fact that there already exists a substantial body of evidence demonstrating that *Acacia sens. lat.* is polyphyletic (Maslin *et al.* 2003; Seigler *et al.* 2006; Murphy 2008). While most species in the Americas and Australia have names available under the new genera, this is not the case for most species in Africa and Asia. Secondly, some concern has been expressed regarding the IBC decision to accept the retypification of *Acacia* (e.g. Rijckevorsel 2006) and it is not known if there will be an attempt to have that decision reversed. In the meantime a sense of uncertainty prevails with respect to the application of the name *Acacia*.

Notwithstanding the above it is desirable to clarify the generic and subgeneric names that should be adopted within *Acacia sens. lat.*, whether the group is treated as a single genus or as multiple genera. The approaches suggested below assume that the IBC decision will prevail.

As already stated, when *Acacia* is treated as a single genus (see Table 1, column 2) there is no subgeneric name available for the former *Acacia* subg. *Acacia* (i.e. the group that contains *A. nilotica*). Therefore, in the absence of a formal subgeneric name it is suggested that this group be referred to as "*Acacia* subgenus 'nilotica group' (= the former subgenus *Acacia*)". As to the 'Australian group' the correct subgeneric name for it is subg. *Acacia*, and under Article 22.1 of the International Code of Botanical Nomenclature, subg. *Phyllodineae* is a synonym of it.

Table 1, column 3 shows what generic names are applicable when *Acacia* is treated as comprising multiple genera, based on the classification as outlined in Maslin *et al.* (2003). Nomenclaturally, the most significant changes apply to "acacias" that occur in Africa, Asia and the Americas where just less than half will become known as *Vachellia* (corresponding to the former *Acacia* subgenus *Acacia*), about half will become known as *Senegalia* (syn. *Acacia* subgenus *Aculeiferum*) and the remainder will be placed in the two small New World genera, *Acaciella* (syn. *Acacia* sect. *Filicinae*) and *Mariosousa* (corresponding to the former "*Acacia coulteri* group"). The genus *Acacia* (syn. *Acacia*

Table 1. Generic and subgeneric names for *Acacia sens. lat.* following decision at the Nomenclature Session of the 17th International Botanical Congress (IBC) in Vienna to endorse and ratify the recommendations of the Committee for Spermatophyta and the General Committee of IAPT to accept the Orchard and Maslin (2003) proposal to retypify *Acacia* with a new type.

Pre-IBC names (*A. nilotica* the type of *Acacia*)	Post-IBC names (*A. penninervis* the type of *Acacia*)	
	Acacia treated as a single genus	*Acacia sens. lat.* treated as multiple genera[1]
ACACIA	**ACACIA**	**VACHELLIA**
Subgenus **Acacia**	Subgenus 'nilotica group'[2]	
Subgenus **Aculeiferum**	Subgenus **Aculeiferum**	**SENEGALIA**
Section Spiciflorae	Section Spiciflorae	
Section Filicinae	Section Filicinae	**ACACIELLA**
Acacia coulteri group	"*Acacia coulteri* group"	**MARIOSOUSA**
Subgenus **Phyllodineae**	Subgenus **Acacia**	**ACACIA**

[1] Number of genera based on information provided in Maslin *et al.* (2003)

[2] Currently there is no name available at the subgeneric level for this taxon

subgenus *Phyllodineae* (DC.) Ser. and *Racosperma* Mart.) is the largest group and is predominantly confined to Australia but is extensively cultivated around the world. Because combinations in *Vachellia* and *Senegalia* have not been made for the African and Asian species it can be problematic if one needs to provide a generic context for these entities. In these cases the following appellations are suggested, using *A. nilotica* as an example: *Acacia* (*Vachellia*) *nilotica* or *A.* (*Vachellia*) *nilotica*.

What is most likely in the future is that the fragmentation of *Acacia sens. lat.* will continue and that names will become available under the new genera (Table 1, column 3) at irregular intervals over a period of time. Furthermore, as noted by Brummitt (2004), it is not inconceivable that more than five genera may ultimately be recognised from within *Acacia sens. lat.* For these reasons the Species Gallery of the Worldwidewattle website (http://www.worldwidewattle.com/) is keeping track of the new names as they are published and for the sake of convenience presents them as 'Alternative' names to *Acacia*. Worldwidewattle also provides users with alternative views of the classification of *Acacia*, namely, single- vs multiple-generic views.

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A review of the classification of *Acacia* (Leguminosae, Mimosoideae)

a235980

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Abstract

This paper reviews the history of the systematics of *Acacia s.l.*, providing a comparison of recent phylogenies to previous classifications, with a focus on *Acacia s.s.* Herein, *Acacia s.s.* is used in the sense of the segregated genus based on *A. penninervis*, and excluding *Senegalia*, *Vachellia*, *Acaciella*, and *Mariosousa*. Problems have been apparent with the classification of *Acacia s.l.* for many years and there is now general recognition that *Acacia s.l.* is polyphyletic. *Acacia s.s.*, a largely Australian group with close to 1000 species, has been shown to be monophyletic. Although molecular phylogenetic studies in recent years have clarified the relationships of some groups within *Acacia s.s.*, this diverse clade lacks a phylogenetic classification. Recent evidence has provided renewed support for the recognition of a redefined section *Pulchelloidea sensu* Vassal, and although formal taxonomic changes at this time are regarded as premature, it has been demonstrated that taxonomic groups in *Acacia s.s.* based upon one or two "key" characters are not monophyletic.

Muelleria 26(1): 10-26 (2008)

Introduction

The genus *Acacia* Miller, if treated in the broad sense, includes c.1450 species (Lewis *et al.* 2005, p. 3) with species in Africa, the Americas, Asia and Australia, and forms the second most speciose genus in the family Leguminosae after *Astragalus* (Maslin 1988; Mabberley 1997). If treated in the strict sense following the re-typification of *Acacia* with an Australian type (Orchard & Maslin 2003; Maslin 2008), *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*), includes 987 species (see Fig. 1 for distribution) with 975 species in Australia (Maslin 2004), and is still the second largest legume genus by a considerable margin (Lewis *et al.* 2005). *Acacia s.s.* comprises the largest genus of plants in Australia (Maslin 1995). No species currently occur in New Zealand, although fossil evidence suggests that the genus was once present there (Guinet 1981; Martin 1994). Several species of *Acacia s.l.* are common in the Middle East, and references to members of the genus date from early in recorded history. For example, the ancient Egyptians had a hieroglyphic symbol for *Acacia*, and the Bible describes the Ark of the Tabernacle as being made of *Acacia* wood (Moldenke & Moldenke 1952). It is not surprising that a group of plants known from such early times has such a long and complex systematic history.

Herein the segregated generic names for *Acacia s.l.* will be used following the re-typification of *Acacia* with an Australian type, namely: *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*), *Vachellia* (formerly *Acacia* subgenus *Acacia*), *Senegalia* (formerly *Acacia* subgenus *Aculeiferum s.s.*), *Acaciella* (formerly *Acacia* subgenus *Aculeiferum* section *Filicinae*), and *Mariosousa* (formerly *Acacia* subgenus *Aculeiferum* "Acacia coulteri group"). Further explanation of these names and their application can be found in Maslin (2008). However, when comparing alternative classifications and results, the original names used by each author are retained (where possible), to simplify the summary of the original literature.

In recent times the need for a phylogenetically based classification of *Acacia s.l.*, to guide workers in a variety of fields, has become increasingly apparent. Examples include studies of host-parasite co-evolution (Crespi *et al.* 2004); plant physiology (Pohlman 2005; Warwick & Thukten 2006);

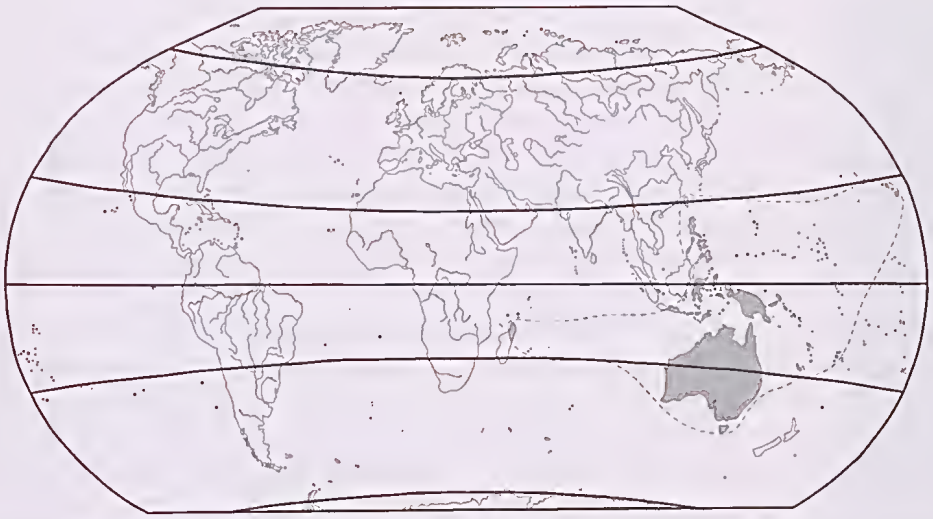

Figure 1. Distribution map of *Acacia s.s.*, also described as the "Australian group" (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*).

and rhizobial interactions and atmospheric nitrogen fixation (Brockwell *et al.* 2005). Because it is such a large and heterogeneous group, *Acacia s.s.* has a particular need for an infrageneric classification based on phylogenetic principles. Currently the most frequently used classification, of Pedley (1978), combines earlier schemes, such as those of Bentham (1875) and Vassal (1972), in an attempt to create a pragmatic system (Maslin 2001). This classification was adopted (albeit slightly altered, with section *Alatae* not recognised) by Maslin (2001), in the comprehensive *Flora of Australia* treatment of *Acacia s.s.* Maslin (2001) acknowledged that this was not a phylogenetically based classification, but it provided a pragmatic subdivision of the genus. In this paper an overview of previous classifications of *Acacia s.l.* is provided. There have been several recent reviews (e.g. Chappill & Maslin 1995, Maslin & Stirton 1997, Maslin 2001, Maslin *et al.* 2003a, 2003b) and this paper aims to extend these reviews to take into account the results of recent molecular systematic studies. New molecular analyses have increased our knowledge of the phylogeny of *Acacia s.l.* dramatically (notably Luckow *et al.* 2003; Murphy *et al.* 2000, 2003, 2005; Miller *et al.* 2003a, 2003b; Brown *et al.* 2006; Ariati *et al.* 2006). The aim of this paper is to provide a review of the systematics of *Acacia s.l.*, with a particular focus on *Acacia s.s.*, with a guide to pertinent literature on systematics, classification and recent phylogenetic analyses. In order to follow the complex nomenclature, a table comparing the main classification schemes and a broad comparison of ranks and names is provided for *Acacia s.s.* (Table 1).

Mimosoideae: some background

Acacia s.l. is placed in the legume subfamily Mimosoideae, in tribe Acacieae (Lewis 2005). In the latest comprehensive classification of Leguminosae, the Mimosoideae comprise c. 3270 species in four tribes (Lewis *et al.* 2005), rather than the five tribes recognised in Mimosoideae (Bentham 1875; Elias 1981) until recently. Some recent morphological and molecular datasets have supported the monophyly of the Mimosoideae (Chappill 1995; Käss & Wink 1996; Dayanandan *et al.* 1997; Lavin *et al.* 2005), characterised by regular (actinomorphic) flowers with valvate petals often fused at the base and compound pollen with porate apertures (Polhill *et al.* 1981; Guinet 1981). Chappill (1995) listed a number of morphological synapomorphies found in most (but not all) taxa in the Mimosoideae clade, including bipinnate leaves, abaxial position of the median petal, valvate petal aestivation, prominently exserted stamens, four celled polyads and absence of a stylar groove. However, Elias (1981), and

Table 1. A comparison of the classification schemes of *Acacia* s.s. (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*) by Bentham (1875), Vassal (1972), Pedley (1978), Pedley (1986), Maslin and Stirton (1997) and Maslin (2001), modified from Chappill and Maslin (1995) and Murphy *et al.* (2003). Where possible equivalent groups (at different ranks) are aligned from left to right across table. This comparison has not been possible to maintain between all classifications, and some incongruities are noted in square brackets. Abbreviations: gen. = genus; ser. = series; subser. = subseries; subg. = subgenus; sect. = section; subsect. = subsection.

Bentham (1875)	Vassal (1972)	Pedley (1978)	Pedley (1986)	Maslin and Stirton (1997)	Maslin (2001)
	subg. *Heteraphyllum*	subg. *Phylladineae*	gen. *Racasperma*	subg. *Phylladineae*	subg. *Phylladineae*
	(Syn subg. *Phylladineae*)				
ser. ***Batrycephalae***		sect. *Batrycephalae*	sect. *Racasperma* [synanymy includes sections *Phylladineae*, *Alatae* and *Batrycephalae* of Pedley (1978)]	sect. *Batrycephalae*	sect. *Batrycephalae*
ser. ***Pulchellae***	sect. *Pulchellaidea*	sect. *Pulchellae*	sect. *Pulchellae*	sect. *Pulchellae*	sect. *Pulchellae*
ser. ***Phylladineae***					sect. *Phylladineae*
subser. *Alatae*	subsect. *Parviscutellae*	sect. *Alatae*		sect. *Alatae*	
subser. *Cantinuae*	subsect. *Magniscutellae*				
subser. *Uninerves*	sect. *Uninervea*	sect. *Phylladineae*		sect. *Phylladineae*	
				a. "Racemase species"	
				b. "Non-racemase species"	
subser. *Plurinerves*	sect. *Heteraphyllum*	sect. *Plurinerves*	sect. *Plurinervia*	sect. *Plurinerves*	sect. *Plurinerves*
subser. *Pungentes*	subsect. *Glabulifarae*			a. "Micraneuraus species"	
				b. "Oliganeuraus species"	
subser. *Calamifarmes*					
subser. *Juliflarae*	subsect. *Spiciferae*	sect. *Juliflarae*		sect. *Juliflarae*	sect. *Juliflarae*
				a. "Micraneuraus species"	
				b. "Oliganeuraus species"	
subser. *Bruniaideae*	[rank not used]	sect. *Lycapadiifaliae*	sect. *Lycapadiifalia*	sect. *Lycapadiifalia*	sect. *Lycapadiifalia*

Luckow *et al.* (2000) found that the Mimosoideae are not monophyletic due to uncertainty surrounding the relationships of some taxa of the *Dimorphandra* group of Caesalpinioideae, and a number of other studies have found Caesalpinioideae to be paraphyletic (Chappill 1995; Käss & Wink 1996; Doyle *et al.* 1997). The distinction between taxa in the Caesalpinioideae and Mimosoideae is not well defined and further phylogenetic analysis is required to clarify this boundary (Luckow *et al.* 2005a).

Mimosoideae were traditionally composed of five tribes: Parkieae, Mimozygantheae, Mimoseae, Ingeae and Acacieae (Bentham 1875; Elias 1981). *Acacia s.l.* species make up over one third of the members of the Mimosoideae (Cowan 1998). All five tribes were characterised by floral features, although the genera included in each tribe have often changed according to the interpretations of different authors. It is notable that the "defining characters" may not be present in all genera assigned to a particular tribe. Elias (1981) defined the Parkieae as having an imbricate calyx in the bud (although in that volume *Parkia* and *Pentaclethra*, were mistakenly noted as having valvate aestivation of the calyx lobes). Parkieae were further characterised by sepals united into a tube, five or ten stamens with staminodia, and anthers with or without an apical gland. DNA sequence data from the *rbc*L gene have been insufficient to resolve the relationship of Parkieae to the other tribes in the Mimosoideae (Käss & Wink 1996; Dayanandan *et al.* 1997). Luckow *et al.* (2000) found that Parkieae was polyphyletic, with *Pentaclethra* removed from *Parkia* at a basal node in the Mimosoideae, and both genera are now known to be related to different genera in the Mimoseae (Luckow *et al.* 2005a). In the classification of Luckow (2005) this has resulted in the inclusion of both *Pentaclethra* and *Parkia* in the Mimoseae and the abandonment of Parkieae as a tribe. The tribe Mimozygantheae was characterised by imbricate free sepals, ten functional stamens and no anther gland; it is monotypic, containing only *Mimozyganthus carinthus*. Unlike Parkieae, Mimozygantheae was retained in Lewis *et al.* (2005) despite recent molecular phylogenetic results showing this genus to be nested in Mimoseae, sister to *Prosopidastrum*.

The remaining three large tribes of Mimosoideae traditionally recognised comprise: the Mimoseae, which were characterised by valvate calyx aestivation and twice as many stamens as petals (Lewis & Elias 1981); the Ingeae, which had valvate calyx lobes and numerous stamens fused into a tube (Nielsen 1981; for a full overview see Brown 2008); and the Acacieae, which were characterised by an indefinite number of stamens (more than 10) that are free or united only at the base and a calyx that is valvate in the bud (Elias 1981; Vassal 1981). These features, however, are not unique to the tribe. In fact, no single morphological character distinguishes Acacieae from other tribes in subfamily Mimosoideae, and this has called into question the monophyly of Acacieae and the other tribes in the Mimosoideae (Chappill & Maslin 1995). Chappill and Maslin (1995) found members of the Mimoseae to be sister to a clade containing Parkieae, Ingeae and Acacieae, although they acknowledged that many characters were missing in their analysis. Acacieae includes *Acacia s.l.*, and the monotypic genus *Faidherbia* A. Chev., although there is some ongoing debate as to whether *Faidherbia* is better placed in the tribe Ingeae (Elias 1981; Guinet 1990; Lewis & Rico-Arce 2005).

Species of *Acacia s.l.* are generally trees or shrubs; some African and American species, however, have a scandent habit (Ross 1981). Most have free staminal filaments, although some African and American species have filaments that are shortly united at the base. Much debate has centred around whether *Acacia s.l.* is monophyletic or if it contains multiple lineages and should be split into more than one genus (e.g. Pedley 1986; Maslin *et al.* 2003b). Chappill and Maslin (1995) found *Acacia s.l.* to be paraphyletic based on morphological and chemotaxonomic characters, but they did not recommend taxonomic revision until further research had been completed because such a split would require far-reaching nomenclatural changes (Maslin 1987, 1988; Chappill & Maslin 1995). In the past decade it became clear that any attempt to resolve the relationships of *Acacia s.l.* needed to include members of other Mimosoideae tribes, in particular the Ingeae (Chappill & Maslin 1995; Grimes 1995; Robinson & Harris 2000). It was not until more comprehensive sampling of the other tribes in Mimosoideae was done, that Ingeae and Mimoseae were also recognised as non-monophyletic (Luckow *et al.* 2003; Miller *et al.* 2003b). It has recently been found, on the basis of molecular phylogenetic analyses, that the tribal system of

Mimosoideae is in need of complete revision, with the current tribes polyphyletic or paraphyletic (Luckow *et al.* 2003). The non-monophyly of Acacieae and Ingeae are particularly problematic, with the recognition of monophyletic taxa requiring the generic revision of *Acacia s.l.* (Miller *et al.* 2003b). This has contributed to a highly controversial debate about the application of the name *Acacia* (Pedley 1986; Maslin *et al.* 2003a; 2003b, Luckow *et al.* 2005b). The recent classification of Mimosoideae presented in Lewis *et al.* (2005) was a stop-gap measure and recognised four rather than five tribes in Mimosoideae, mainly based on the results of Luckow *et al.* (2000 and 2003). In other respects the Lewis *et al.* (2005) classification largely retains the scheme of Elias (1981) in recognising the four tribes, Mimoseae, Mimozygantheae, Ingeae and Acacieae, but not Parkieae, despite acknowledgment that these tribes (apart from the monotypic Mimozygantheae) are not monophyletic. It is evident that the higher level classification of the Mimosoideae is still fluid pending further comprehensive phylogenetic analysis, but in the meantime the tribal system of Elias (1981) remains a helpful communication device.

A review of the systematic history of *Acacia s.l.*

Early systematic history

The name *Acacia* has been utilised in herbals since the 14th century and was used by Linnaeus as a genus in 1747. These references, however, predate 1753, the starting point of modern botanical nomenclature, and therefore have no formal taxonomic standing today (Ross 1980). Philip Miller (1754) is the author of the name *Acacia*. The original diagnosis included 24 species in the genus and described *Acacia* as having:

"...a tubulous flower, consisting of one leaf, with many stamina or threads, which are many of them collected into a kind of sphere or globe: the pointal of the flower afterward becomes a pod, in which are included several seeds, each of which is separated by transverse diaphragms, and are generally surrounded with a sweetish pulp" (Miller 1754).

This description was broad, and many species described under *Acacia* in Miller's time are no longer recognised as belonging to *Acacia s.l.* today (Ross 1973). A survey of the pre-Linnean history of *Acacia s.l.* was provided by Ross (1980).

Subsequent to Miller, the number of species in *Acacia s.l.* grew rapidly as many taxonomists named and listed new species. For practical reasons it was soon necessary to subdivide the genus into infrageneric groups. Willdenow (1806) listed 102 species of *Acacia s.l.* and recognised seven groups based on the vegetative characters of foliage type and stipule presence. Willdenow's primary groupings were based on whether the foliage was simple (phyllodinous), pinnate, or bipinnate. Sprengel (1826) included 188 species in *Acacia s.l.* These were divided into three unranked groups according to foliage, in a similar manner to Willdenow (1806). In 1825, de Candolle recognised 258 species in *Acacia s.l.* and divided these into four sections. New (1984), reported that de Candolle used only leaf characters in his classification, but de Candolle in fact recognised these sections on the basis of both floral and foliage characters. As already noted by Pedley (1987a), de Candolle's concept of *Acacia s.l.* was somewhat less confused than Willdenow's, due to the former's use of inflorescence type, but a third of the species listed by both authors are no longer recognised in *Acacia s.l.*

Wight and Arnott (1834) segregated *Acacia farnesiana* into a new genus, *Vachellia*. This separation was clearly based on the distinctive pod of this species, although Pedley (1986) suggested that Wight and Arnott gave no reason for the split. Pedley (1987a) observed that this split began a trend to fragment *Acacia s.l.* which would have resulted in taxonomic chaos were it not for Bentham.

Bentham and *Acacia s.l.* taxonomy in the 19th century

In 1841, Bentham began to re-organise Mimosoideae (which he ranked as a suborder of Leguminosae), recognising Acacieae as one of three tribes. In a series of papers published in the period 1842–1846, Bentham initially recognised ten genera in Acacieae (Bentham 1842a, 1842b, 1844a, 1844b, 1845, 1846). Subsequently, he made radical changes to this classification, restricting Acacieae to one genus, *Acacia s.l.*, and creating the new tribe Ingeae to delimit the other nine genera (Bentham 1865).

Bentham (1842a, 1842b) was the first to clearly restrict the boundaries of the genus *Acacia*, advocating floral characters to define a more natural group. Previous authors had used the presence of a dry, two-valved pod to distinguish *Acacia s.l.* Bentham described

this as an inconvenient and uncertain character due to the absence of pods on herbarium material. By excluding from *Acacia s.l.* all species with definite stamens or filaments connected in a cylindrical tube, Bentham created a much more tightly delimited group than his predecessors, and his concept of *Acacia s.l.* was essentially the same as that used today.

Within *Acacia s.l.*, Bentham (1842a) listed 432 species and defined six series: *Phyllodineae, Botrycephalae, Pulchellae, Gummiferae, Vulgares* and *Filicinae*. These series were based primarily on "leaf" or foliage characters and the presence of either stipular spines or prickles (prickles have no vascular tissue, unlike stipules). In his final revision of the genus, Bentham (1875) maintained the above classification (see Table 1), although he raised some unranked groupings within the series *Phyllodineae* to subseries level and reduced the five subseries in *Vulgares* to four. Bentham's subseries were based on inflorescence or vegetative characters and although Bentham did refer to the groups within *Acacia s.l.* as "subgenera" (Bentham 1875, p. 354), in effect predicting what future workers would conclude c. 100 years later, he conformed to the rules governing taxonomic ranks at that time and used the rank of series.

Bentham's classification remained almost intact for the next century and grew to accommodate over twice the number of species. It has been the basis for most subsequent re-arrangements of *Acacia s.l.* (e.g. Guinet 1969; Vassal 1972; Pedley 1978, 1986), and these have, in essence, been re-alignments of Bentham's series, based on changing ideas of taxonomic ranks.

The early 20th century

Bentham was the last taxonomist to revise all known species in *Acacia s.l.* (Pedley 1987a). Since then, authors have propo sed changes to infra-generic groups by examining either a limited range of species within previously named sections of *Acacia s.l.* or species in a particular geographic region. In the first half of the 20th century this resulted in two notable challenges to Bentham's (1875) classification.

Britton and Rose (1928) divided *Acacia s.l.* into 12 genera using pod characters of American species. This system was abandoned after Rose's death in 1934, and species described transferred back to *Acacia s.l.* Pedley (1986) wrote that Britton and Rose's classification was most likely rejected due to problems with recognising genera based on pod characters, and Maslin (1988) described their treatment as "excessive". Britton and Rose renamed Bentham's series *Filicinae* as the genus *Acaciella*, and Pedley (1987b) also later accepted this as a probable distinct genus. *Acaciella* has recently been reinstated and new taxa described within it by Rico Arce and Bachman (2006).

Newman (1932) criticised Bentham's (1875) classification as being "too static" (although he did not explain what this meant) and proposed dividing *Acacia s.l.* into three unranked groups on the basis of a hierarchy of three characters: inflorescence type (racemes, clusters or single inflorescences), flower-groups (cylindrical shaped spikes, oblong spikes or globular heads) and foliage type (bipinnate leaves, phyllodes or absence of leaves). Newman's system was rejected by subsequent authors. New (1984) described it as clearly unnatural, and Pedley (1978) considered it hardly worthy of serious consideration. Newman did, however, recognise the need for a natural classification of *Acacia s.l.*

The second half of the 20th century

Since the 1960s a number of authors have proposed changes to Bentham's (1875) classification, most notably Vassal (1972) and Pedley (1978, 1986) (Table 1). These changes have broadly corresponded to the series and subseries of Bentham, although putatively based more on relationships (although non-cladistic) than those of previous authors.

The classifications undertaken in the past c.40 years were triggered by Guinet's (1969) monumental pollen studies of the polyads of 250 species across all *Acacia s.l.* From this study, Guinet concluded that Bentham's series could be placed into groups based on pollen types. All *Acacia s.l.* are characterised by compound pollen, with a varying number of individual pollen grains. Three pollen types were distinguished by Guinet (1969, 1990):

1. Colporate type: an exine with well-developed columellae and complex apertures composed of a furrow in the external exine and a pore in the internal exine below the furrow.
2. Simple porate type: exine sometimes with weakly developed collumellae. The apertures are simple circular pores on the angles of the distal faces of the pollen grains.

3. Extraporate type: as in the simply porate type, the exine sometimes with weakly developed collumellae and simple pores. The extraporate type is distinguished by false furrows (pseudocolpi) present on the distal faces of the pollen grains.

Guinet (1969) found that the colporate type only occurred in (Bentham's) series *Gummiferae*. The simple porate type was in series *Filicinae*, *Vulgares* and some *Phyllodineae*, while the extraporate type was in *Pulchellae*, *Botrycephalae*, most *Phyllodineae* and some *Vulgares*. Guinet (1986, 1990) later extended his work to cover c. 900 taxa in *Acacia s.l.* Pollen data played an important role in subsequent studies of the systematics of *Acacia s.l.* (Vassal 1972, 1981; Ross 1973; Pettigrew & Watson 1975; Guinet & Vassal 1978; Pedley 1978, 1986), but have been relatively neglected in recent years. Molecular systematics results have not yet been well integrated with the pollen data of Guinet (1969, 1986, 1990).

1. Vassal: three subgenera within *Acacia s.l.*

Vassal (1972) used pollen data, in conjunction with his own work on morphology and ontogeny of seeds and seedlings, to formalise Guinet's (1969) groups. Vassal divided *Acacia s.l.* into three subgenera: subg. *Acacia*, subg. *Aculeiferum* and subg. *Heterophyllum* (although Ross (1981) showed that the name *Phyllodineae* has priority over *Heterophyllum*). These subgenera have formed the conceptual backbone of subsequent classifications (e.g. Guinet & Vassal 1978; Pedley 1978, 1986). Vassal's (1972) groupings are comparable to Bentham's (1875) series, which, as already observed by Pedley (1978), was fortunate, since many of the characters Vassal used for his classification – such as seedling and pollen morphology – are not easily observable. Following Guinet (1969), Vassal (1972, 1979) referred the African species *Acacia albida* to the monotypic genus *Faidherbia* on the basis of its distinctive pollen morphology (polyads with 30 grains compared to 16 grains in all but one African species) and its unique seedling ontogeny (it produces bipinnate leaves from the outset – all other species first develop pinnate leaves). Vassal (1972), however, did not remove *Faidherbia* from the Acacieae, contrary to Guinet's (1969) assertion that it would be better placed in the Ingeae because it was, in his opinion, not closely related to the genus *Acacia s.l.* Vassal (1981) maintained *Faidherbia* in the Acacieae, although Elias (1981) in the same volume stated that the genus was better placed in the Ingeae. This argument has not been finally resolved, although in the classification of Lewis and Rico-Arce (2005), *Faidherbia* is included in the Ingeae.

Vassal's (1972) subgenus *Acacia* corresponds to Bentham's (1875) series *Gummiferae*, and is now treated as genus *Vachellia*. This group has a pantropical distribution and comprises about 200 species, with most occurring in Africa and South America, although 9 species occur naturally in Australia (Kodela & Wilson 2006). Vassal defined this subgenus on the presence of stipular spines and bipinnate leaves (characters also used by Bentham), as well as colporate-type pollen.

Vassal (1972) did not have enough data to include *Filicinae* in his study, but in Guinet and Vassal (1978), *Filicinae* was placed in subgenus *Aculeiferum* with Bentham's (1875) series *Vulgares*. Subgenus *Aculeiferum* has a pantropical distribution similar to subgenus *Acacia*. Only two species are indigenous to the Cape York Peninsula in Australia, and another two species have become naturalised in northern Australia (Ross 2001). Vassal (1972) defined subgenus *Aculeiferum* as having bipinnate leaves, simple porate pollen (although some species of *Vulgares* have extraporate pollen), prickles and an absence of stipular spines. He recognised three sections within subgenus *Aculeiferum*, but studied only 16 out of approximately 150 species (Conn *et al.* 1989).

Vassal's (1972) subgenus *Phyllodineae* comprised Bentham's (1875) series *Botrycephalae*, *Phyllodineae* and *Pulchellae*. These were described by Guinet (1969) as the "Australian group" and are largely confined to that continent (see Fig 1). Pollen in this subgenus is extraporate or sometimes simple porate, spinescent stipules are rare and prickles absent. The foliage may be bipinnate or phyllodinous. Vassal (1972) defined three sections in this subgenus, which combined subseries from Bentham's series *Phyllodineae* (members of which Vassal split into two sections) and *Botrycephalae*. Vassal's (1972) section *Pulchelloidea* included a heterogeneous arrangement of species from Bentham's (1875) series *Phyllodineae* and *Pulchellae* (excluding "plurinerved" species), based on seed and seedling characters. This reclassification included both bipinnate and phyllodinous species in *Pulchelloidea*.

2. *Acacia s.l.* studies prior to phylogenetic analyses

Pettigrew and Watson (1975) conducted a phenetic analysis of Australian *Acacia s.s.* (subgenus *Phyllodineae*) species and recommended disbanding Vassal's section *Pulchelloidea*. Their study showed that the phyllodinous species in this section were similar to species in Vassal's section *Phyllodineae*. However, in agreement with Vassal (1972), the bipinnate-leaved species in Bentham's series *Pulchellae* were found to be different from those in the *Botrycephalae*. Pettigrew and Watson (1975) suggested that Bentham's series *Pulchellae* is related to the phyllodinous subseries *Plurinerves*, and although they did not give an alternative to the placement of Bentham's series *Pulchellae*, they did recognise Vassal's sections *Phyllodineae* and *Uninervea* as coherent groups.

Pedley (1978) supported Pettigrew and Watson's (1975) conclusions that the *Uninervea* are a natural group, although he stated that their study was marred by some errors in identification. Guinet *et al.* (1980) addressed the problems Pettigrew and Watson (1975) identified regarding sect. *Pulchelloidea*. Guinet *et al.* provided evidence from adult morphology, pollen morphology, seed and seedling morphology and seed amino acids that supported Vassal's 1972 acceptance of Bentham's series *Pulchellae*. They disagreed with Pettigrew and Watson's (1975) assertion that the *Pulchellae* are closely related to subseries *Plurinerves*; instead they reaffirmed acceptance of Vassal's sect. *Pulchelloidea* containing phyllodinous and bipinnate species. Vassal and Rouane (1987) reanalysed the groupings within subgenus *Phyllodineae* on the basis of juvenile characters and found further evidence to support Vassal's 1972 groups. In a statistical analysis they found two clusters of species, one corresponding to Vassal's section *Heterophyllum* and the other to section *Pulchelloidea*.

A study of free amino acids in the seeds of 106 species of *Acacia s.l.* (Evans *et al.* 1977) also supported Vassal's 1972 division of *Acacia s.l.* into three subgenera. This study showed that species in subgenus *Acacia* contained the marker amino acid N-acetyldjenkolic acid, which was not found in subgenera *Aculeiferum* and *Phyllodineae*. The latter both contained the same combinations of marker amino acids: S-carboxyethylcystein, S-carboxyisopropylcystein, albizzine and a-amino-ß-acetylaminopropionic acid. Subgenus *Phyllodineae* was distinguished by the presence of an additional amino acid, a-amino-ß-oxalylaminopropionic acid. These data provided evidence that subg. *Phyllodineae* and subg. *Aculeiferum* are more closely related to each other than to subg. *Acacia*. Evans *et al.* (1977) disagreed with Vassal's (1972) transfer of *A. albida* into the genus *Faidherbia* and argued that amino acid data warranted its inclusion in *Acacia* subg. *Aculeiferum*.

Tindale and Roux (1969, 1974) conducted studies of the two main groups of flavonoids (the resorcinol type and the pyrogallol type) in the heartwood and bark of *Acacia s.s* (subg. *Phyllodineae*). In subg. *Phyllodineae*, Tindale and Roux found pyrogallol flavonoids in Bentham's subseries *Plurinerves* and *Juliflorae* and resorcinol flavonoids in series *Botrycephaleae*, *Phyllodineae* subser. *Brunioideae* and some ser. *Uninerves* (those with racemose inflorescences). A combination of both types of flavonoids were found in subg. *Phyllodineae* subseries *Continuae*, *Pungentes*, *Calamiformes* and the remaining *Uninerves*. Thus, Tindale and Roux's (1969, 1974) work supported Vassal's (1972) sect. *Uninervea* (which contained Bentham's sections *Botrycephalae* and *Uninerves* with racemose inflorescences) due to the presence of resorcinol. Tindale and Roux considered pyrogallol flavonoids as originating from a resorcinol type precursor and therefore regarded resorcinol as being 'primitive'. Guinet and Vassal (1978) supported this interpretation and considered sect. *Uninervea* as 'primitive' within subg. *Phyllodineae*. Pedley (1978), however, disagreed and proposed that it is equally likely that the 'primitive' group contained both flavonoid types. Tindale and Roux (1975) also hypothesised, based on a study of African species, that subg. *Acacia* was less "advanced" than subg. *Aculeiferum* because resorcinol flavonoids are most prevalent in subg. *Acacia* and less common in subg. *Aculeiferum*. In contrast, Ross (1973, 1981) found that a greater number of species in subg. *Acacia* displayed polyploidy, a character which he regarded as being more 'advanced'.

In an attempt to clarify the confusion surrounding 'primitive' and 'advanced' characters, Guinet and Vassal (1978) conducted an intuitive (non-cladistic) study of the "level of specialisation" within *Acacia s.l.* They examined pollen, chromosome number, the morphology of seeds, seedlings, pods, inflorescences and vegetative characters. Characters were divided into three states – unspecialised, specialised and highly specialised

– and applied to each of the subgenera recognised by Vassal (1972). From this information total levels of specialisation were estimated. Guinet and Vassal (1978) found that subg. *Acacia* was the most specialised and subg. *Aculeiferum* the least specialised. Ross (1981) and Pedley (1986) criticised the arbitrary size classes for the three states, and Pedley (1986) also disagreed with some of the evolutionary polarities to which the character states were assigned. For example, Pedley countered the interpretation that small seeds are unspecialised by giving evidence that seed predation may make smaller seeds an advanced state.

3. Pedley's splitting of *Acacia s.l.* and the ensuing controversy

Pedley (1978, 1979), in his first revision of *Acacia s.l.*, assessed the data of Vassal (1972), chemical data from Tindale and Roux (1969, 1974, 1975) and Evans *et al.* (1977) and information on chromosome numbers, hairs, stipules, leaf, glands, inflorescences, flowers, pod and seed characters. Pedley (1978) recognised three subgenera that corresponded to those of Vassal (1972), but his scheme differed in the arrangement of sections within the three subgenera, ostensibly to make his classification more usable. Pedley (1978) advocated a more agglomerative approach than Vassal (1972) and reinstated some of Bentham's (1875) subseries within subgenus *Phyllodineae*. Pedley also named three sections in subg. *Acacia* instead of Vassal's two. The main differences, however, between Pedley (1978) and Vassal (1972) reside in subg. *Phyllodineae*. Pedley created the new section *Lycopodiifoliae* to include species with phyllodes in whorls with interspersed stipules. These species were originally included in subser. *Brunioideae* Bentham, but were not studied by Vassal (1972). Pedley (1978) regarded uninerved and plurinerved phyllodes as the basis for a fundamental division in subg. *Phyllodineae*. Maslin (1988), disagreed, and gave examples of single species that may vary between uninerved and plurinerved states. However, Maslin (Maslin & Stirton 1997; Maslin 2001) later accepted there is a fundamental division between uninerved and plurinerved species. Pedley's (1978) infrageneric groups are those commonly used today (see Table 2 for a simplified key).

Pedley (1981), using data similar to those of his 1978 study but placing more emphasis on pollen, seedling and chemical characters, recommended splitting the genus into *Acacia*, (containing only subg. *Acacia*), and a genus "Z", which would include subg. *Phyllodineae* and subg. *Aculeiferum*. Later Pedley (1986), formally split *Acacia s.l.* into three genera, applying and resurrecting earlier generic names; subg. *Acacia* became genus *Acacia*, subg. *Phyllodineae* became *Racosperma* Martius and subg. *Aculeiferum* became genus *Senegalia* Rafinesque. The split was widely criticised at the time, despite Pedley's (1986, 1987b, 1987c) attempts to justify his scheme on the basis that many other large plant groups (such as Casuarinaceae) were in the process of similar changes.

Table 2. A simplified key to the classification of *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*) by Pedley (1978) (adapted from Maslin 1995 and Arjati 2006).

1 Leaves (mature plants) reduced to phyllodes or scales, or absent	
2 Flowers arranged in cylindrical spikes	Section *Juliflorae*
2: Flowers arranged in globular or oblongoid heads	
3 Branchlets winged by decurrent phyllodes	Section *Alatae*
3: Branchlets not winged	
4 Phyllodes arranged in whorls	Section *Lycopodiifoliae*
4: Phyllodes not in whorls	
5 Phyllodes 1-nerved per face (4-7 nerved when terete or quadrangular)	Section *Phyllodineae*
5: Phyllodes more than 1-nerved per face (8 or more nerved when terete or quadrangular)	Section *Plurinerves*
1: Leaves of mature plants bipinnate	
6 Heads arranged in elongated racemes	Section *Botrycephalae*
6: Heads or axillary peduncles solitary	Section *Pulchellae*

Pedley (1986) stated that phylogeny and biogeography were being hampered by the acceptance of *Acacia s.l.* as a large, heterogeneous genus.

Maslin (1988), opposed Pedley's (1986) classification on the basis that the data Pedley used to change his interpretation in the years 1978 to 1986 were not significant enough to support such a substantial alteration. Maslin (1988) stated that Pedley (1986) incorrectly placed greater emphasis on certain characters to upgrade the infrageneric ranks in *Acacia s.l.* and was unduly influenced by trends in other plant groups. He maintained that Pedley's proposal was premature and more information was needed before any changes to the genus were made. Vassal (1988) supported Maslin's criticism of Pedley (1986), claiming that too many uncertainties remained in the recognition of coherent groups within *Acacia s.l.* Consequently, Pedley's (1986) concept and split of *Acacia s.l.* was not widely accepted until recent molecular results resolved many of the uncertainties (e.g. Miller *et al.* 2003b).

One aspect of Pedley's (1986) classification that was accepted was his suggestion that there had been an independent derivation (polyphyly) of at least two groups within *Acacia s.l.* Pedley (1986) thought subg. *Acacia* forms one group and subg. *Aculeiferum* plus subg. *Phyllodineae* (*Senegalia* plus *Racosperma*) the other. Only recently has it been possible to identify the closest relatives to these groups outside the tribe Acacieae . At the time, Guinet (1990) stated that pollen morphology clearly isolated subg. *Acacia* from the rest of the genus and placed it closer to the tribe Mimoseae. In contrast, Pedley (1986) regarded subg. *Aculeiferum* and subg. *Phyllodineae* as most closely related to the tribe Ingeae. This has been supported by recent results of Luckow *et al.* (2003). The relatively recent realisation that some taxa placed within *Acacia s.l.* were more closely related to other members of the Mimosoideae was a critical breakthrough (Chappill & Maslin 1995; Grimes 1995). Testing the monophyly of the three genera/subgenera of *Acacia s.l.*, and determining the sister relationships of these groups has become the goal of recent research.

Phylogenetic analyses of *Acacia s.l.*

The main reason why confusion previously surrounded the classification of *Acacia s.l.* was the lack of comprehensive cladistic analyses to investigate the phylogenetic relationships both within the genus and at a higher level. As a first step, Playford *et al.* (1992) conducted a small comparative study of the 5S spacer ribosomal DNA in seven *Acacia s.l.* species and used cladistic methods to analyse their results. However, their study was deficient in sampling genera outside *Acacia s.l.* and therefore could not resolve any of the questions raised by Guinet (1990) and Pedley (1986). Playford *et al.*'s (1992) study found three paralagous copies of the 5S spacer rDNA units in the *Acacia s.l.* species they studied, making any analysis of the relationships between the three subgenera difficult. However, they did conclude that subg. *Phyllodineae* formed a cluster separate to subg. *Acacia* plus subg. *Aculeiferum*.

Chappill and Maslin (1995) used a morphological and chemical dataset to examine the tribal status of Acacieae in relation to other taxa in the Mimosoideae, as well as infrageneric relationships of *Acacia s.l.* Chappill and Maslin's (1995) generic analysis concluded that the tribe Acacieae was polyphyletic. *Faidherbia* and subg. *Acacia* nested within the Ingeae, whereas subg. *Aculeiferum* and subg. *Phyllodineae* were sister taxa and sister to the tribe Ingeae + *Faidherbia* and subg. *Acacia* clade. Thus, Chappill and Maslin (1995) proposed a unification of the tribes Acacieae and Ingeae, as suggested by Guinet (1969) on the basis of pollen morphology. However, Chappill and Maslin (1995) also conducted an 'infrageneric analysis', in which they found subg. *Aculeiferum* to be paraphyletic. A clade containing members of subgen. *Aculeiferum* section *Aculeiferum* and one exemplar of section *Monacanthe* was sister to a monophyletic subg. *Phyllodineae*. In this analysis *Faidherbia* was nested within subg. *Aculeiferum*, and subg. *Acacia* formed a clade. However at the basal node of the cladogram a clade of subgen. *Acacia* was unresolved with respect to a clade of tribe Ingeae taxa and another clade containing subgenera *Aculeiferum* and *Phyllodineae*. Robinson and Harris (2000) criticised the results of Chappill and Maslin (1995), remarking that their "generic" and "infrageneric" cladograms are contradictory in their placement of subg. *Acacia* and subg. *Aculeiferum*. The major limitation of Chappill and Maslin's (1995) dataset was the large proportion of missing data (approximately 28% in the infrageneric analysis), which can severely affect the number of equally parsimonious trees found in a cladistic analysis

(Kitching *et al.* 1998). In the only other substantial morphological cladistic analysis of the tribe Ingeae and tribe Acacieae, Grimes (1999) found that Acacieae was polyphyletic, with *Faidherbia* and. subg. *Aculeiferum* and subg. *Acacia*, nested within tribe Ingeae. Subgenus *Phyllodineae* was sister to that (tribe Ingeae + subg. *Aculeiferum*/subg. *Acacia* + *Faidherbia*) clade.

Robinson and Harris (2000) used plastid DNA restriction fragment length polymorphisms (RFLPs) to examine the phylogeny of *Acacia s.l.* and the relationship of taxa of tribe Acacieae to taxa in tribe Ingeae. Robinson and Harris (2000) included 59 species of *Acacia s.l.*, seven species of tribe Ingeae, *Faidherbia* and one species of tribe Mimoseae in their study. The main sampling limitation was the number of taxa sampled from subg. *Phyllodineae* (*Acacia s.s.*): six species from only four of the seven sections were sampled. They found subg. *Phyllodineae* to be monophyletic and nested within a clade containing tribe Ingeae. *Faidherbia* was found to be sister to this clade. Robinson and Harris also found that both subg. *Acacia* and subg. *Aculeiferum* were monophyletic and sister groups.

Bukhari *et al.* (1999) obtained a different result from both Chappill and Maslin (1995) and Robinson and Harris (2000). They also used plastid RFLPs, but in contrast to Robinson and Harris (2000), they found subg. *Acacia* was sister to subg. *Phyllodineae*, and this clade was sister to another clade containing *Faidherbia* nested within subg. *Aculeiferum*. Bukhari *et al.* (1999) did not include any other members of the Mimosoideae in their analysis, precluding the possibility of finding sister group relationships of *Acacia s.l.* to taxa outside the tribe Acacieae.

Miller and Bayer (2000, 2001) conducted molecular phylogenetic analyses using chloroplast (*trn*K/*mat*K) and nuclear (histone H3-D) DNA sequences. Their studies included taxa from tribes Acacieae and Ingeae, and a few tribe Mimoseae taxa. Miller and Bayer found that the Ingeae were paraphyletic by inclusion of a monophyletic *Acacia s.s.* They also found that *Faidherbia* was sister to the *Acacia s.s.* + Ingeae clade and subg. *Acacia* (*Vachellia*) was monophyletic and sister to *Neptunia*, to a member of the Mimoseae. Subgenus *Aculeiferum* was paraphyletic, with *A. boliviana* (section *Filicinae*) resolved at the basal node, sister to the ingroup.

More recently, with greater sampling of diversity in the tribes Ingeae, Acacieae and Mimoseae and the use of multiple chloroplast DNA regions, greater congruence has been found between the studies by Luckow *et al.* (2003) and Miller *et al.* (2003b). These studies have shown that subg. *Acacia* (*Vachellia*) is well supported as monophyletic and related to members of tribe Mimoseae, well removed from other members of *Acacia s.l.* or tribe Ingeae. The tribe Ingeae and members of subg. *Aculeiferum s.l.* were paraphyletic. *Acacia s.s.* was strongly supported as monophyletic and nested amongst tribe Ingeae, although its relationship to members of tribe Ingeae was unresolved.

Phylogenetic relationships within *Acacia s.s.* and comparison with earlier classifications

In recent years and in multiple analyses (Chappill & Maslin 1995; Grimes 1999; Bukhari *et al.* 1999; Robinson & Harris 2000; Miller & Bayer 2000, 2001; Luckow *et al.* 2003; Miller *et al.* 2003b) most of the possible combinations of relationships between the three subgenera in *Acacia s.l.* and the tribe Ingeae have been hypothesised. The recent use of DNA sequence data has provided more congruent results and the clear realisation that *Acacia s.s.* is monophyletic. There have now been a number of recent phylogenetic studies that have focussed on this, mostly Australian, clade, however, little was known about the relationships of taxa within this large heterogeneous arrangement of species (Chappill & Maslin 1995; Bukhari *et al.* 1999; Robinson & Harris 2000; Miller & Bayer 2000, 2001). *Acacia s.s.* is generally divided into seven sections (Pedley 1978; see Table 2). However, uncertainty has surrounded infrageneric groups (Bentham 1875; Vassal 1972; Pedley 1978, 1986), and at least one section, *Alatae*, was thought not to be monophyletic by Maslin and Stirton (1997). Chappill and Maslin (1995) found that the classification within subg. *Phyllodineae* needed to be re-assessed. Vassal's (1972) sect. *Pulchelloidea* was not supported in their analysis, and none of Pedley's (1978) sections within subgenus *Phyllodineae* were resolved as monophyletic.

There is currently no phylogenetically based classification of *Acacia s.s.* despite the size, conspicuousness and importance of the group within Australian ecosystems (Hnatiuk & Maslin 1988, Maslin 2001). The sheer size of *Acacia s.s.*, with over 975 species, makes a comprehensive analysis of the whole genus

difficult. It is likely that the approach of examining the phylogeny of smaller groups of taxa will incrementally improve knowledge, and by using DNA datasets, such as chloroplast and nuclear ribosomal (ITS and ETS) DNA sequences (e.g. Murphy *et al.* 2000, 2003; Ariati *et al.* 2006; Brown *et al.* 2006) it has been possible to build on previous studies. This approach is only limited by the relative informativeness of molecular markers at different taxonomic levels. Some conclusions on relationships within *Acacia* s.s can now be made, although it is currently premature to undertake formal taxonomic changes.

For comparative purposes the studies of *Acacia* s.s. below will be discussed in light of the sections of Pedley (1978). Although it is difficult to compare the various phenetic and cladistic analyses that have been conducted over the last 40 years with more recent DNA based phylogenies – due to limited overlap of sampling and differing methods – some congruence of results is now apparent. The sections in *Acacia s.s.*, which were defined by Bentham (1875) and later re-aligned by Pedley (1978) and subsequent workers (see Table 1), are now known to be largely unnatural but form a pragmatic and easily used system (Maslin 2001). The groups defined by Vassal (1972) (not including sect. *Lycopodiifoliae* which were not considered in that study), are similar to the groups defined by Pedley (1986). Both Vassal (1972) and Pedley (1986) amalgamated the *Botrycephalae* with section *Phyllodineae* into one section, and the *Plurinerves* and *Juliflorae* into another section, to form two very large sections (Table 1). However, their treatments differed in the classification of the remaining taxa in *Acacia* s.s., especially sections *Alatae* and *Pulchellae*.

Overall, four main groups of taxa have been resolved in recent molecular phylogenies using DNA sequences (e.g. Murphy *et al.* 2000, 2003, 2005; Miller *et al.* 2003a). These groups are briefly outlined below and followed by more detailed comparisons to the results of previous studies:

- A clade comprising sections *Lycopodiifoliae*, *Alatae*, *Pulchellae* and some *Phyllodineae*. This group is probably one of the most significant findings of recent years because it provides support for a similar group to Vassal's (1972) sect. *Pulchelloidea*.
- A large clade containing species with plurinerved phyllodes, in sections *Juliflorae* and *Plurinerves*, and many uninerved taxa (sect. *Phyllodineae*), more typically the non-racemose species.
- Nested within the above plurinerved clade is a smaller clade containing all members of sect. *Botrycephalae* and some members of sect. *Phyllodineae*, typically those with racemose inflorescences (Brown *et al.* 2006).
- Recently two clades of mostly arid zone taxa have been resolved. These groups contain species related to *Acacia victoriae*, *Acacia pyrifolia* (the "Acacia victoriae clade") and *Acacia murrayana* (the "A. murrayana clade"). While these taxa form two well supported clades, their placement in relation to other taxa in *Acacia* s.s. remains equivocal (Ariati *et al.* 2006).

Pulchelloidea clade

Within *Acacia* s.s. only one section, sect. *Lycopodiifoliae*, has been supported as monophyletic. The other sections were found to be non-monophyletic or there was not enough information to confirm or refute a hypothesis of monophyly. Section *Lycopodiifoliae* (Bentham's subseries *Bruniodeae*), which have phyllodes in whorls, are morphologically distinct from other taxa in *Acacia s.s.* Rutishauser (1999) demonstrated that the phyllode and stipule whorls in sect. *Lycopodiifoliae* are developmentally unique and Pedley (1987a) suggested that it was likely that sect. *Lycopodiifoliae* would be segregated from subg. *Phyllodineae*, although it is now apparent that the segregation of sect. *Lycopodiifoliae* would leave *Acacia* s.s. paraphyletic (Murphy *et al.* 2003). However, so far the monophyly of sect. *Lycopodiifoliae* has not been thoroughly explored. Chappill and Maslin (1995), in their morphological analysis, used a single representative from this section, and found that it grouped with taxa in sect. *Plurinerves*. In contrast, Brain and Maslin (1996), using serological data, concluded that sect. *Lycopodiifoliae* may be closely related to sect. *Juliflorae*. The study by Brain and Maslin (1996) was the most comprehensive molecular study of *Acacia* s.s. prior to recent DNA sequence analysis, although the serological method was limited by the requirement for simultaneous analysis of samples. Vassal (1972) did not include any representatives of sect. *Lycopodiifoliae* in his study. Pettigrew and Watson (1975) conducted

a phenetic analysis, using the classification of Vassal (1972), and found that members of sect. *Lycopodiifaliae* grouped together. It was unclear, however, in Pettigrew and Watson's (1975) analysis whether sect. *Lycapadiifoliae* grouped with Vassal's (1972) sect. *Uninervea* (containing sections *Phylladineae* and *Batrycephalae*) or sect. *Heterophyllum* (containing sections *Juliflorae* and *Plurinerves*).

Section *Pulchellae* are also morphalogically distinct, with bipinnate foliage and often with stipular spines (Guinet *et al.* 1980). Somewhat surprisingly sect. *Pulchellae* have not been confirmed as monophyletic (e.g. Murphy *et al.* 2003; Miller *et al.* 2003a). However, like sect. *Lycopodiifoliae* the sampling of sect. *Pulchellae* has been limited in molecular analyses. Vassal's (1972) sect. *Pulchellaidea* was based on seedling, pollen and other morphalagical characters (including spinescent stipules), and included members of sections *Pulchellae*, *Alatae* and other taxa from sect. *Phyllodineae*. Chappill and Maslin (1995) thought it likely that the only groups to be monophyletic were the two sections with bipinnate foliage, sect. *Botrycephalae* and sect. *Pulchellae*, although both these sections were unresolved in their morphological analysis. Chappill and Maslin (1995) found that sect. *Pulchellae* grouped in a clade with some members of sections *Alatae* and *Phylladineae* with non-racemose inflorescences. Brain and Maslin (1996) found "no strang relationship" of sect. *Pulchellae* with any other graup in subg. *Phyllodineae* but a weak association between sect. *Alatae* and taxa in sections *Plurinerves*, *Juliflarae* and *Phyllodineae*. Maslin and Stirton (1997) concluded that sect. *Alatae* is an unnatural graup.

Plurinerved taxa

Most members of *Acacia s.s.* have plurinerved phyllades (sect. *Juliflorae* and sect. *Plurinerves*) but unfortunately there has been very little resolution of relationships of these taxa in phylogenetic studies. Although most plurinerved taxa are found in a single clade, their monophyly has not been supported by sequence data. DNA sequence studies have found a large clade, containing most members of sections *Juliflorae* and *Plurinerves* and members of sect. *Phyllodineae* and *Botrycephalae* (Murphy *et al.* 2003; Miller *et al.* 2003a). However, there is little resolution within this large clade, apart from the relationship of sections *Botrycephalae* and *Phyllodineae* with racemose inflorescences (described below). While many studies have found a natural division between taxa with single-nerved phyllades (sect. *Phyllodineae*) and those with plurinerved phyllades (Vassal 1972; Pettigrew & Watson 1975; Pedley 1986; Chappill & Maslin 1995; Maslin & Stirton 1997; Miller & Bayer 2000), Brain and Maslin (1996) did not find a clear distinction between the uninerved and plurinerved taxa using serological data. Additionally, there has not yet been any phylogenetic study that supports the informal groupings of oligneurous and microneurous taxa. These are taxa with differing arrangements of minor secondary nerves in their phyllodes, in sections *Juliflarae* and *Plurinerves* (Maslin & Stirton 1997, see Table 1).

Batrycephalae

A close relationship of taxa from sect. *Batrycephalae* to taxa in sect. *Phylladineae* with racemose inflorescences was hypothesised in a number of earlier studies, such as those using: flavonoid chemistry (Tindale & Raux 1969, 1974), morphalagy (Vassal 1972; Chappill & Maslin 1995) and more recently DNA sequence data (e.g. Murphy *et al.* 2000). The large-scale phylogenies of *Acacia s.s* by Murphy *et al.* (2003) and Miller *et al.* (2003a) provided increased evidence for the relationship of sect. *Botrycephalae* to some taxa in sect. *Phylladineae*, and it was confirmed by Brown *et al.* (2006), whose comprehensive analysis showed that sect. *Botrycephalae* is polyphyletic, and nested within sect. *Botrycephalae* are taxa of sect. *Phyllodineae* with racemose inflorescences.

Much speculation has focussed on whether bipinnate leaves in mature plants are plesiomorphic in *Acacia s.s.* because adult bipinnate foliage is a widespread character in subfamily Mimosoideae (Guinet and Vassal 1978; Mound and Crespi 1999). Mapping of morphological characters onto molecular phylogenies does not support the conclusion that adult bipinnate foliage is plesiomorphic (Murphy *et al.* 2000, 2003, Miller *et al.* 2003a). The only bipinnate sections, *Botrycephalae* and *Pulchellae*, are not sister groups and are both nested within clades of phyllodinous taxa, which indicates that two separate reversals to bipinnate leaves have occurred (Murphy *et al.* 2003). The reversal to bipinnate foliage (compound leaves) may be interpreted as neotenous, since the ontogeny of phylladinous taxa includes a

pinnate phase (Pedley 1986). Pedley (1986) recognised that sect. *Botrycephalae* may be neotenic because of the occurrence of transitional taxa, such as *A. latisepala* Pedley, which only sometimes produce phyllodes.

Conclusion

Problems have been apparent in the systematics and classification of *Acacia s.l.* for many years (Maslin & Stirton 1997). Early literature was centred on taxonomic lists of *Acacia s.l.* species without consideration of relationships between the taxa. However, Bentham (1875) created a classification of *Acacia s.l.* that was robust enough to last almost a century, although concerns over the last thirty years have necessitated revision of this classification. Vassal (1972) recognised three subgenera within *Acacia s.l.* Pedley (1986) revised the genus and formalised three genera corresponding to Vassal's subgenera, but this reclassification was regarded as premature at the time of its publication, and other workers advised caution before such an important nomenclatural decision was made (Maslin 1988; Vassal 1988; Chappill & Maslin 1995). Chappill and Maslin (1995) published the first cladistic analysis of the genus, in which they recognised *Acacia s.l.* as paraphyletic and stated that their findings lent support to previous authors' suggestions (such as those of Guinet 1969 and Pedley 1981) and proposals (Pedley 1986) to divide *Acacia s.l.* into more than one genus. In recent years the polyphyly of *Acacia s.l.* has been well demonstrated and the monophyly of *Acacia s.s.* supported (Luckow *et al.* 2003; Miller *et al.* 2003b; Murphy *et al.* 2003). It has been recognised that a phylogenetic classification of *Acacia s.s.* is required (e.g. Maslin & Stirton 1997, Maslin 2001), and molecular phylogenetic studies of recent years have clarified the relationships of groups within *Acacia s.s.* (Miller *et al.* 2003a, Murphy *et al.* 2003). However, further studies with increased sampling across the diversity of *Acacia s.s.*, and additional molecular markers are required to provide a comprehensive understanding of the phylogeny of *Acacia s.s.* and to resolve clades for a revised classification. In the past, single morphological characters or combinations of characters, such as the number of phyllode nerves and inflorescence characters, have been used to define groups in *Acacia s.s.* (Bentham 1875; Vassal 1972; Pedley 1978; Maslin & Stirton 1997). It has now been found that taxonomic groups in *Acacia s.s.* based upon one or two "key" characters are not monophyletic and the characters used to define them are homoplasious.

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Systematics of the tribe Ingeae (Leguminosae-Mimosoideae) over the past 25 years

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What are the Ingeae?

The tribe Ingeae is a large group of legumes in the subfamily Mimosoideae, with close to 1000 species, in 36 genera (Lewis & Rico Arce 2005). It is distributed pantropically (Fig. 1) and only one macromorphological character differentiates it from tribe Acacieae: stamens united into a tube (Ingeae) rather than being free (Acacieae; Elias 1981). There are some exceptions to this rule, however, with several species of the Acacieae (*Acacia sens. lat.*) having stamens fused at the base, although not always forming a tube as in the Ingeae, e.g. *Acacia adengonia* (Pedley) R.S.Cowan & Maslin (Australia: WA), *Ac. eriocarpa* Brenan (Africa), *Ac. ogadensis* Chiov. (Africa), *Ac. stipulata* DC. (Australia: NT and WA), and species of the '*Vachellia* group' (Vassal 1981; Cowan & Maslin 1990). In addition, some ingioid taxa, including several species of *Havardia* Small and at least one species of *Lysiloma* Benth., have stamens that are virtually free to the base (Barneby and Grimes 1996). The main centre of diversity of tribe Ingeae is in Southern and Central America, with a secondary centre in Asia–Australia (SE Asia–Pacific Islands–Australia).

Bentham established the tribe Ingeae in 1865, recognising nine genera, primarily on characters of the legume (Bentham 1865): *Affonsea* A.St.-Hil., *Albizia* Durazz., *Archidendron* F.Muell., *Calliandra* Benth., *Enterolobium* Mart., *Inga* Mill., *Lysiloma*, *Pithecellobium* Martius and *Serianthes* Benth. In 1875 Bentham revised the suborder Mimosaceae, at that time recognising the Ingeae as being made up of 15 genera/subgenera. This revision has been the basis of all others since, despite the fact that "no firm concepts of genera were established" because of a lack of material with fruits (Nielsen 1981a: 173). Since Bentham (1875), many taxa have been described and the generic concepts of the Ingeae have changed frequently (see Nielsen 1981a for a summary table of generic changes). This nomenclatural instability within tribe Ingeae, a group of economic importance that is widely used in the Americas and Asia for agro-forestry, shade trees for crops, fuel wood, land reclamation and stock feed, has resulted in much confusion for foresters, ecologists and conservationists (Hughes 1997).

The most recent classification scheme for the Ingeae was presented in the 'Legumes of the World' (Lewis & Rico Arce 2005). This was an

Abstract

The large tropical tribe Ingeae (Leguminosae–Mimosoideae) is one of the most poorly studied groups of legumes, with a complex and unstable taxonomic history. In the first volume of 'Advances in Legume Systematics' in 1981, Nielsen presented a revision of the tribe Ingeae, which compared all previous systems and presented a new classification for the tribe. In subsequent years, numerous taxonomic changes were proposed as a result of monographs and revisions of genera and regional groups. During this time, two somewhat incongruent classification schemes arose, creating much taxonomic confusion. These two schemes were merged in a recent classification; however, many taxonomic problems and questions remain to be answered. This paper summarises the changes and conflict in the taxonomy of the tribe over the past 25 years, based primarily on the two major regional revisions: the Neotropics by Barneby and Grimes, and SE Asia, Australia and the Pacific Islands by Nielsen, Guinet and Baretta-Kuipers. Current understanding of phylogenetic relationships of the tribe is also reviewed.

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Figure 1. Distribution of tribe Ingeae. The general area that the Ingeae are distributed in is shaded in grey.

amalgamation of the two, sometimes contradictory, regional classifications (see below) that emerged after the revision of the tribe by Ivan Nielsen in 1981. Numerous taxonomic changes were proposed in regional revisions and generic monographs after Nielsen's 1981 classification. This paper aims to summarise these changes, highlighting areas where current classification systems are incongruent, and presents current phylogenetic knowledge of this large, diverse group of legumes.

Taxonomy of the Ingeae

Nielsen's 1981 classification

Nielsen (1981a) briefly described and compared the previous classifications of the Ingeae, from Bentham (1875) through to Hutchinson (1964), and concluded that only eight genera from these systems were universally accepted — *Albizia*, *Calliandra*, *Cedrelinga* Ducke, *Enterolobium*, *Inga*, *Lysiloma*, *Serianthes* and *Wallaceodendron* Koord. — with the remaining taxa being placed in the genus *Pithecellobium*. Prior to Nielsen's (1981a) classification, which was based on vegetative, floral, as well as carpological characters, classifications primarily reflected pod characteristics, resulting in what have been called 'pod-genera'. Therefore, the redefinition of many genera and the transfer of many species were necessary.

Nielsen (1981a) listed twenty-one genera in the tribe (Table 1): *Abarema* Pittier, *Affonsea*, *Albizia*, *Archidendron*, *Calliandra*, *Cedrelinga*, *Cojoba* Britton & Rose, Genus A, Genus B, Genus C, Genus D, *Havardia*, *Enterolobium*, *Inga*, *Klugiodendron* Britton & Killip, *Lysiloma*, *Marmaroxylon* Killip, *Pithecellobium*, *Punjuba* Britton & Rose, *Serianthes*, *Wallaceodendron*, and *Zygia* P.Browne. However, in the abstract he noted there were only "about 17 genera". This discrepancy can be explained by the exclusion of the four unnamed genera (Gen. A, B, C, D) and *Punjuba*, which was listed with unknown affinity. Nielsen (1981a) also presented a key to the 21 genera.

Many of the taxonomic changes proposed by Nielsen (1981a) relate to his treatment of two genera, *Albizia* and *Pithecellobium*, which had long been dumping grounds for difficult taxa. He chose to recognise *Pithecellobium* in the strict sense, recognising 20 species in the genus, in addition to several segregate genera formerly placed in *Pithecellobium* (see Nielsen 1981a), for example, *Cojoba*, *Klugiodendron*, Genus D, and *Zygia*. One species of *Pithecellobium sens. lat.* was left with unknown affinity: *Pithecellobium incuriale* (Vell.) Benth. (=*Leucochloron* Barneby & J.W.Grimes). Bentham placed *Pithecellobium incuriale* in *Pithecellobium* sect. *Samanea* ser. *Coriaceae*, however, Nielsen (1981a) did not include it with the other species formerly in this section ('Genus D' sensu Nielsen 1981a) because of its differing floral morphology.

Albizia, on the other hand, was treated by Nielsen (1981a) in a broad sense (the broadest concept of *Albizia* in the history of the tribe), including many genera that were previously segregated from *Pithecellobium*, such as *Cathormion* Hassk., *Chloroleucon* (Benth.) Britton & Rose, *Macrosamanea* Britton & Rose, *Pseudosamanea* Harms and *Samanea* Merr. This decision was primarily based on pod characteristics; however, characteristics of the seed and wood were also discussed in relation to some of the inclusions. As well as transferring a number of taxa into *Albizia*, Nielsen (1981a) segregated two former sections of *Albizia*, sect. *Lophantha* ser. *Pachyspermae* Benth. and sect. *Spiciflora* Benth. as distinct genera: Genus A and Genus B, respectively.

Cathormion and *Samanea* were included in *Albizia* by Nielsen (1981a) because he noted that it was impossible to distinguish boundaries between these taxa and *Albizia* sect. *Albizia*, with intermediate pod forms found between the dehiscent, membranous, and unsegmented pods of *Albizia lebbeck* (L.) Benth. and the segmented and indehiscent pods of *Cathormion umbellatum* (Vahl) Kosterm. Intermediate forms were also found between the pods of *Cat. umbellatum* and those of *Samanea saman* (Jacq.) Merr., which break away in 1-seeded segments. Despite the pollen characteristics of *Chloroleucon* being more similar to *Enterolobium*, and Nielsen's view that "perhaps it might be best regarded as a genus", it was included in *Albizia* because that is where it will "key out" (Nielsen 1981a: 182).

The inclusion of *Macrosamanea* and *Pseudosamanea* in Nielsen's *Albizia* is puzzling, especially because the "wood anatomy of *Pseudosamanea guachapele* differs greatly from that of *Albizia*" (Nielsen 1981a: 182). In addition, these two genera were considered by Nielsen (1981a: 182) to be "in the same alliance" as *Enterolobium*, however, he kept *Enterolobium* as a separate genus even though the boundary between it and *Albizia* was noted to be "not too sharp" (Nielsen 1981a: 182).

Nielsen (1981a) also considered *Abarema*, *Lysiloma* and *Enterolobium* to be closely related to the broadly circumscribed *Albizia*. *Abarema*, the only other genus identified in the '*Albizia* group' was distinguished from *Albizia* by red colouration on the inside of the pods, bird pollination, contorted to straight pods, and the funicle often slightly dilated. *Lysiloma* and *Enterolobium* were not included in the '*Albizia* group', although both were considered almost identical to *Albizia* by Nielsen (1981a). It appears that *Enterolobium* was only retained as a distinct genus, as it was by authors before him, because it is well known and widely cultivated in the tropics (Nielsen 1981a).

Since Nielsen's 1981 classification, taxonomic revisions of the Ingeae have generally focused on two broad geographical regions: the Neotropics (Barneby & Grimes 1996; Barneby & Grimes 1997; Barneby 1998) and SE Asia, Australia and the Pacific Islands (Nielsen *et al.* 1983; Nielsen *et al.* 1984a,b; Nielsen 1985; Nielsen 1992; Cowan 1998). Classifications of the tribe have also been presented in several new family-wide systems since 1981 (Polhill 1994; Lewis & Rico Arce 2005). A comparison of how genera have been treated in these various regional and familial classifications is presented in Table 1.

Regional revisions since 1981

Numerous generic monographs of the Ingeae were completed through the 1980s and 1990s. Nielsen continued his work on Ingeae focusing on taxa in SE Asia, the Pacific Islands and Australia (Nielsen *et al.* 1983; Nielsen *et al.* 1984a,b; Nielsen 1985). Barneby and Grimes (1996; 1997) and Barneby (1998) revised all of the Neotropical taxa except *Enterolobium* and *Lysiloma*, which were only briefly described as these had been monographed in two PhD dissertations (see Mesquita 1990 & Thompson 1980 in Barneby & Grimes 1996), and *Inga* (including *Affonsea*) and *Zapoteca* H.M.Hern. because these taxa were being treated by Pennington (1997) and Hernández (1986; 1989), respectively.

SE Asia, the Pacific Islands and Australia

The genera found in SE Asia, the Pacific Islands and Australia are: *Albizia*, *Archidendron*, *Archidendropsis* I.C.Nielsen, *Cathormion*, *Pararchidendron* I.C.Nielsen, *Paraserianthes* I. C. Nielsen, *Pithecellobium*, *Samanea*, *Serianthes*, *Thailentadopsis* Kosterm. and *Wallaceodendron*. Revisions of these Ingioid taxa in the region were predominantly completed by Nielsen, many in collaboration with Guinet and Baretta-Kuipers (Nielsen *et al.* 1983; 1984a,b; Nielsen 1985), culminating in an account of the Mimosaceae for the Flora Malesiana (Nielsen 1992). Genera recognised in Flora Malesiana, which incorporates information from the precursory

Table 1. Generic comparison between classification schemes from 1981 until present. For earlier generic classifications see Nielsen (1981). Square parentheses are used, where necessary, to highlight the different generic concepts of different authors. —, taxa not treated in that publication. Regional revisions: Nielsen (1992), SE Asia, Australia and the Pacific Islands; Barneby & Grimes (1996-1997), the Neotropics. Familial classifications: Polhill (1994); Lewis & Rico (2005).

Ingeae genera[A]	Nielsen (1981)	Nielsen (1992)[B]	Polhill (1994)	Barneby & Grimes (1996–98)	Lewis & Rico (2005)
Abaremo	*Abarema*	—	*Aboremo*	*Abarema*	*Aborema*
Affonseo	*Affansea*	—	*Inga*	*Inga*	*Inga*
Albizia	*Albizia*	*Albizio*	*Albizia*	*Albizio*	*Albizio*
Archidendran	*Archidendron*	*Archidendron*	*Archidendron*	—	*Archidendron*
Archidendrapsis	Genus B	*Archidendropsis*	*Archidendropsis*	—	*Archidendropsis*
Balizia	*Albizia*	—	—	*Balizia*	*Albizia*
Blanchetiadendran	*Albizia* or *Pithecellobium*?	—	—	*Blonchetiadendran*	*Blanchetiodendran*
Calliondra	*Calliondro*	—	*Colliandra*	*Calliondra*	*Calliondra*
Cathormian	*Albizio*	*Catharmion*	*Cotharmion*	*Cathormion*	*Cathormion*
Cedrelinga	*Cedrelingo*	—	*Cedrelinga*	*Cedrelinga*	*Cedrelingo*
Chloraleucan	*Albizia*	—	*Chloraleucon*	*Chlaraleucon*	*Chlaraleucan*
Cajoba	*Cajoba*	—	*Cajoba*	*Cajaba*	*Cajobo*
Ebenapsis	*Havardio*	—	*Havardia*	*Ebenapsis*	*Ebenapsis*
Enteralabium	*Enteralabium*	—	*Enteralabium*	*Enterolabium*	*Enteralobium*
Faidherbia	—	—	*Faidherbia*	—	*Foidherbia*
Falcataria	Genus A p.p.	*Paraserianthes* p.p.	*Paraserianthes* p.p.	*Falcotoria*	*Falcataria*
Guinetia	—	—	—	—	*Guinetia*
Havardia	*Havardia*	—	*Havardia*	*Havardia*	*Havordia*
Hesperolbizia	*Albizia*	—	*Albizia*	*Hesperolbizia*	*Hesperalbizia*
Hydrachoreo	*Albizia*	—	*Albizia*	*Hydrochorea*	*Hydrachorea*
Inga	*Ingo*	—	*Inga*	*Inga*	*Inga*

Ingeae genera[A]	Nielsen (1981)	Nielsen (1992)[B]	Polhill (1994)	Barneby & Grimes (1996–98)	Lewis & Rico (2005)
Leucochloron	*Pithecellobium incuriole*[C]	—	—	*Leucochlaron*	*Leucochloron*
Klugiodendran	*Klugiadendron*	—	*Abarema*	*Abarema loeta*	*Aborema*
Lysilama	*Lysilama* [c.35 spp.]	—	*Lysilama* [# nat listed]	*Lysilama* [8 spp.]	*Lysilomo* [8–9 spp.]
Macrasamonea	Genus D and *Albizia*	—	*Macrasamanea*	*Macrasamonea*	*Macrasamaneo*
Marmoraxylon	*Mormoraxylon*	—	*Marmaraxylon*	*Zygia*	*Marmaroxylan*
Obalinga	—	—	*Obolinga*[D]	*Cajaba*	*Cajaba*
Painteria	*Havardia*	—	*Havardia*	*Painteria*	*Painteria*
Pararchidendran	Genus C	*Porarchidendran*	*Parachidendran*		*Pararchidendron*
Paraserianthes	Genus A	*Poraserionthes* [4 spp.]	*Paraserionthes*	*Paraserianthes* [1sp. with 4 var.]	*Poraserionthes* [1sp.]
Pithecellobium	*Pithecellobium*	*Pithecellobium*	*Pithecellobium*	*Pithecellabium*	*Pithecellabium*
Punjuba	*Punjuba*	—	*Aborema*	*Abaremo*	*Abarema*
Pseudosamaneo	*Albizia*	—	*Albizio*	*Pseudasamaneo*	*Pseudasomaneo*
Somanea	*Albizia*	*Somanea*	*Samanea*	*Somanea*	*Samanea*
Serianthes	*Serianthes*	*Serianthes*	*Serianthes*		*Serianthes*
Sphinga	*Hovordia*	—	*Havardio*	*Sphinga*	*Sphinga*
Thailentodopsis	*Hovardia*	—	*Havordia*	unplaced: nated ta be from albiziaid stack	*Thailentadapsis*
Viguieronthus	*Colliondra*	—	*Calliandra*		*Viguieronthus*
Wallaceadendron	*Walloceadendran*	*Walloceadendron*	*Wolloceadendran*	—	*Wallaceodendron*
Zapoteca	*Colliondra*	—	*Zapoteca*	*Zapateca*	*Zapateco*
Zygia	*Zygio*	—	*Zygia*	*Zygio*	*Zygia*

[A] The Ingeae genera column includes all genera that have been recognised in the Ingeae from 1981 to 2006

[B] Data in this column is based on the Flora Malesiana but also reflects the precursory work done in Malesia by Nielsen *et al.* (see text for references)

[C] Placed with unknown affinity within the genus *Pithecellobium*

[D] *Obolinga* was described by Barneby (1989) but after morphological phylogenetic analyses it was sunk into *Cojoba* (as *Co. zanonii*)

papers (Nielsen *et al.* 1983; 1984a,b; Nielsen 1985), are listed in Table 1. The Ingeae were also revised for a number of local floras: e.g., Flora of Australia (Cowan 1998), Flora of New Caledonia (Nielsen 1983) and Flora of Cambodia, Laos and Vietnam (Nielsen 1981b). As a result of these works, many taxonomic changes were made from Nielsen's 1981 Ingeae classification. The only genus in the region that has not changed taxonomically since the last revision is *Wallaceodendron* (Nielsen *et al.* 1983; Nielsen *et al.* 1984b; Nielsen 1992).

The 37 species of *Albizia* recognised in SE Asia, the Pacific Islands and Australia were revised in two papers; the first (Nielsen 1979) concentrated on the mainland Asian species, while the second focused on those found in Malesia (Nielsen 1985). In both revisions, and in the Flora Malesiana (Nielsen 1992), a key to the flowering specimens as well as a key to the fruiting specimens were provided. Nielsen (1979; 1985) did not produce an infrageneric classification for the genus *Albizia* because he believed it "would be premature" (Nielsen 1985: 27) without the formal transfers and regional revisions of the American and African species he proposed belonged in *Albizia* in 1981. Nielsen (1985) did, however, employ two informal groups in the Malesian region: '*Albizia corniculata* group' and '*Serialbizia* group'.

One alteration to Nielsen's broad concept of *Albizia* of 1981 was the recognition of *Cathormion* as a distinct genus. At first, Nielsen (1992: 143) noted, of *Cathormion*, that there were "about 12 species in tropical and subtropical South America and Africa, and 1 species in the SE Asia/Australia region". But based on aberrant pollen morphology, he later decided it was preferable to consider *Cathormion* a monotypic genus of SE Asia–Australia (Nielsen 1992: 143).

Archidendron is the largest genus endemic to the SE Asian, Pacific Island and Australian region, with 94 species (Nielsen *et al.* 1984a), and the fourth largest genus in the tribe behind *Inga* (c. 300 spp.), *Calliandra* (135 spp.), and *Albizia* (c. 120-140 spp.; Lewis & Rico Arce 2005). An additional 22 species of *Archidendron* have also been listed as imperfectly known because of a lack of (good) collections or the destruction of types in Berlin (Nielsen *et al.* 1984a). Taxa, in Malesia, that were formerly referred to as *Abarema*, *Zygia* and *Morolobium* Kosterm. have been transferred to *Archidendron* with new combinations made by Nielsen *et al.* (1984a).

An infrageneric classification of the genus *Archidendron* was proposed (Nielsen *et al.* 1984a), recognising eight series based on morphology: *Archidendron* (c. 15 spp.), *Bellae* I.C.Nielsen (4 spp.), *Calycinae* I.C.Nielsen (3 spp.), *Clypeariae* (Benth.) I.C.Nielsen (c. 51 spp.), *Morolobiae* (Kosterm.) I.C.Nielsen (c. 4 spp.), *Pendulosae* (Mohl.) I.C.Nielsen (3–4 spp.), *Ptenopae* I.C.Nielsen (2 spp.) and *Stipulatae* (Mohl.) I.C.Nielsen (c. 12 spp.). A key to these series was presented in the Flora Malesiana treatment (Nielsen 1992: 88), while three identification keys to species were provided in the generic revision (Nielsen *et al.* 1984a): one for all species based on all morphological characters, and two separate keys for the flowering and fruiting specimens of series *Clypeariae*, *Archidendron* and *Bellae*.

Four new genera of Ingeae were described for the SE Asian, Pacific Islands and Australian region (Nielsen 1983; Nielsen *et al.* 1983; 1984b; Barneby & Grimes 1996) — *Archidendropsis*, *Falcataria* (I.C.Nielsen) Barneby & J.W.Grimes, *Pararchidendron* and *Paraserianthes* — and another, *Thailentadopsis*, was resurrected by Lewis and Schrire (2003). Three of the newly described genera had been identified informally in Nielsen's 1981 classification, but were not formalised until the thorough regional revision of Nielsen *et al.* (1983; 1984b). *Archidendropsis* ('Genus B', Nielsen 1981a) was described in the Flora of New Caledonia (Nielsen 1983) for the taxa with winged, thin walled seeds without pleurogram, formerly *Albizia* sect. *Spiciflorae* Benth. ser. *Platyspermae* Benth. The genus is composed of 14 species and has been divided into two subgenera (Nielsen *et al.* 1983): *Archidendropsis* (11 spp.) found in New Caledonia, New Guinea, and New Britain-Solomon Islands; and subgenus *Basaltica* I.C.Nielsen (3 spp.) found only in Australia (Queensland). Nielsen *et al.* (1983) questioned whether subg. *Basaltica* should in fact be a separate genus but based on the uniformity of flowers they decided to retain the group until further data became available.

Pararchidendron ('Genus C', Nielsen 1981a) was originally described by Nielsen (part I; Nielsen *et al.* 1983), with detailed discussion on the taxonomy and morphology presented in part III of those studies (Nielsen *et al.* 1984b). It is a monotypic genus, with four varieties, found in Indonesia (Java, Lesser Sunda Islands, Irian Jaya), Papua New Guinea and Australia (Queensland and NSW). Originally identified as including two species

(*Abarema sumbawaensis* Kosterm. and *Parar. pruinosum* (Benth.) I.C.Nielsen), *Ab. sumbawaensis* was later synonymised as a variety of *Parar. pruinosum* (Nielsen *et al.* 1984b). *Pararchidendron* has affinities to the genus *Archidendron*, differentiated by having alternate leaflets and areolate seeds (Nielsen *et al.* 1984b; Nielsen 1992).

The third new genus, segregated as 'Genus A' by Nielsen (1981a), was *Paraserianthes*. It was described as having four species, one with two subspecies and another with two varieties, and divided into two sections: *Paraserianthes* and *Falcataria* I.C.Nielsen (Nielsen *et al.* 1983). It is native to Australia, Indonesia (Sumatra, Java, Lesser Sunda Islands, Irian Jaya), Papua New Guinea and the Solomon Islands, and is considered related to *Serianthes*, but with opposite leaflets and dehiscent pods (Nielsen 1992). Members of *Paraserianthes* were formerly recognised in a section of *Albizia* (sect. *Lophantha* ser. *Pachyspermae*), however, because of their uniform flowers arranged in ± elongate spikes, they were removed and considered as a distinct genus (Nielsen 1981a).

Barneby and Grimes (1996), in their revision of neotropical Ingeae, promoted Nielsen's *Paraserianthes* section *Falcataria* to generic rank as their genus *Falcataria* and leaving *Paraserianthes* as monotypic. *Paraserianthes falcataria* (L.) I.C.Nielsen is widely planted in the neotropics and this is presumably why the only combination made was *Paras. falcataria* to *Falcataria molucanna* (Miq.) Barneby & J.W.Grimes; no combinations were made for the other two taxa of Nielsen's section *Falcataria*, which are endemic to Papua New Guinea (*Paras. pullenii* (Verdc.) I.C.Nielsen) and Australia (*Paras. toona* (Bailey) I.C.Nielsen). The decision to raise *Falcataria* to generic rank was based on cladistic morphological analyses (Grimes 1995; Barneby & Grimes 1996), which placed *Paras. falcataria* (=*Falcataria molucanna*) in an unresolved polytomy near the base of the Ingeae, while *Paras. lophantha* (Willd.) I.C.Nielsen was the sister group to other SE Asian–Pacific Island–Australian taxa. The generic concept of *Paraserianthes* remains open at this time, however, research into this problem is underway.

The last new genus recognised in the region since 1981 is *Thailentadopsis*, which was resurrected from the genus *Havardia* by Lewis and Schrire (2003). *Thailentadopsis* was originally described as a genus by Kostermans in 1977, and is currently composed of three species — *T. nitida* (Vahl) G.P.Lewis & Schrire, *T. tenuis* (Craib) Kosterm. and *T. vietnamensis* (I.C.Nielsen) G.P.Lewis & Schrire — that "cannot be confidently placed in any other currently accepted ingioid genera" (Lewis & Schrire 2003: 492). Nielsen (1981a) recognised these three species in a broadly defined *Havardia*, while Barneby and Grimes (1996) provisionally excluded them from *Havardia*, leaving them with the generic name *Pithecellobium* but later hypothesising "that they form a phylogenetically distinct group derived from a primitive albizioid stock" (Barneby & Grimes 1997: 3). The relationship of *Thailentadopsis* to other ingioid genera remains unknown, although, Lewis and Schrire (2003) note that the monotypic *Cathormion* is morphologically the most similar. They also indicate that the relationship to the three Asian species of *Calliandra* (see 'Other regions' for discussion of these Asian species of *Calliandra*) should be investigated.

The last native SE Asian, Pacific Island and Australian genus to discuss is *Serianthes*. A detailed revision of the genus was conducted after the 1981 tribal revision (Nielsen *et al.* 1983; 1984b), and *Serianthes* is now recognised as comprising about 18 species, with several other insufficiently known taxa identified but not formally described (Nielsen *et al.* 1983; 1984b; Nielsen 1992). An infrageneric classification based on the structure of the inflorescence and pods (Nielsen 1992) has also been proposed, with the genus divided into two subgenera (Nielsen *et al.* 1983), *Minahassae* I.C. Nielsen and *Serianthes*, the latter further divided into two sections, *Serianthes* and *Calycina* I.C.Nielsen.

Species of *Pithecellobium* and *Samanea* are found in the SE Asian, Pacific Islands and Australian region, however, they are either cultivated, weedy or naturalised. All species referred to the genus *Pithecellobium* in the region have now been moved to *Archidendron* and *Albizia* (Nielsen *et al.* 1984a; Nielsen 1992), with the exception of *Pi. dulce* (Roxb.) Benth., which was introduced to the Philippines from Mexico, and later introduced to India where it was first described (Nielsen 1992). *Samanea saman* is widely planted throughout the region and is now "appearing spontaneous all over the tropics" (Nielsen 1992: 156).

The Neotropics

Extensive revisions of taxa from the Neotropics have also been undertaken since Nielsen's 1981 tribal classification, predominantly by Barneby and Grimes (1996; 1997) and Barneby (1998) but with generic revisions by others (see Mesquita 1990 & Thompson 1980 in Barneby & Grimes 1996; Pennington 1997; Rico Arce *et al.* 1999). The revisions of Barneby and Grimes (1996; 1997) and Barneby (1998) primarily focused on the taxa that had been referred to the genus *Pithecellobium* at one time or other; keys are presented for all genera. After all generic revisions, 25 genera were recognised in the neotropics, including two newly described genera and the resurrection of two genera from *Pithecellobium*: *Abarema*, *Albizia*, *Balizia* Barneby & J.W.Grimes, *Blanchetiodendron* Barneby & J.W.Grimes, *Calliandra*, *Cedrelinga*, *Chloroleucon*, *Cojoba*, *Ebenopsis* Britton & Rose, *Enterolobium*, *Guinetia* L.Rico & M.Sousa, *Havardia*, *Hesperalbizia* Barneby & J.W.Grimes, *Hydrochorea* Barneby & J.W.Grimes, *Inga*, *Leucochloron* Barneby & J.W.Grimes, *Lysiloma*, *Macrosamanea*, *Painteria* Britton & Rose, *Pithecellobium*, *Pseudosamanea*, *Samanea*, *Sphinga* Barneby & J.W.Grimes, *Zapoteca*, and *Zygia*.

The taxonomy of *Cedrelinga*, *Enterolobium* and *Lysiloma* has remained almost the same since Nielsen's tribal revision (1981a). The affinities of the monotypic *Cedrelinga* remain unknown, although it has been suggested to be closely related to *Albizia*, *Enterolobium* section *Enterolobium* and the *Zygia* group (Barneby & Grimes 1996). *Enterolobium* remains a distinct genus, as it was in Nielsen (1981a), and was revised by Mesquita (1990 in Barneby & Grimes 1996) who recognised nine species. Barneby and Grimes (1996) generally agreed with Mesquita's treatment but in addition described one new species (*En. oldemanii* Barneby & J.W.Grimes) and a new section (sect. *Robrichia* Barneby & J.W.Grimes). The generic concept of *Lysiloma* remains as it did in Nielsen (1981a), however, Nielsen recognised about 35 species, while Barneby and Grimes (1996) only recognised eight species (Table 1). This difference is a result of strikingly different species delimitation of these authors, particularly in relation to a number of characters that are relatively plastic, such as, leaf-formula, pubescence, and width of pod (Barneby & Grimes 1996).

The taxonomic concepts of *Abarema*, *Cojoba*, *Inga* and *Zygia* have all been expanded in the past 25 years (Barneby & Grimes 1996; 1997; Pennington 1997). *Klugiodendron* and *Punjuba* were transferred to *Abarema* based on cladistic morphological analysis (Barneby & Grimes 1996). However, *Abarema* is now defined by a combination of homoplasious characters and "can no longer be easily defined in exact terms" (Barneby & Grimes 1996: 43). *Cojoba* has been expanded to include the monotypic genus *Obolinga* Barneby based on cladistic morphological analysis (Barneby & Grimes 1997). When *Obolinga* was described by Barneby (1989) the carpological syndromes of it and *Cojoba* were considered too different to be congeneric. However, the unique fruit type of *Obolinga* has since been found in a species of *Cojoba*, *Co. bahorucensis* J.W.Grimes & R.G.Garciá, and based on the phylogeny in Barneby and Grimes (1997), both species are nested well within the latter genus.

Species of *Inga* are found throughout the wet Neotropics and the genus contains about 300 species, including up to 50 that are imperfectly known and also taxa formerly placed in the genus *Affonsea* (Pennington 1997). *Affonsea*, which was recognised as a distinct genus by Nielsen (1981a), was originally excluded from *Inga* because of its multicarpellate ovary, however, in all other respects *Affonsea* and *Inga* are the same. Since 1981, a multicarpellate ovary has also been found in several species of *Inga* (Pennington 1997), hence the incorporation of *Affonsea* into *Inga*.

The inclusion of *Marmaroxylon* into a more broadly defined *Zygia* by Barneby and Grimes (1997) was not unexpected, as Nielsen (1981a) noted they may be congeneric. While a cladistic analysis of *Zygia* (including *Marmaroxylon*) was not undertaken, because more than one third of the species are still unknown in fruit, Barneby and Grimes (1997) did divide the genus into nine sections.

The neotropical element of *Albizia* sensu Nielsen is the generic concept in the region that has changed the most since the 1981 classification because Barneby and Grimes (1996) adopted a generic concept of *Albizia* that is considerably narrower that that of Nielsen (1981a). The American species of *Albizia* were revised by Barneby and Grimes (1996) and they developed an infrageneric classification of these species. Based on cladistic morphological analyses they reinstated *Pseudosamanea*, *Samanea* and *Chloroleucon*, which

Nielsen (1981a) synonymised under *Albizia*, and described three new genera from *Albizia* sensu Nielsen (Barneby & Grimes 1996): *Balizia*, *Hesperalbizia*, and *Hydrochorea*. However, Rico Arce did not agree with *Balizia*, sinking it back into *Albizia*, and noting that "it seems wiser to adopt a broader concept of the genus *Albizia* until the genus has been monographed across its range" (Rico Arce 1999: 555). *Albizia* is still in need of a worldwide revision.

Macrosamanea was recognised as a South American genus of zygioid affinity composed of 11 species by Barneby and Grimes (1996), while Nielsen (1981a) synonymised it under *Albizia*. The genus was originally described by Britton and Killip in 1936 based on taxa from *Pithecellobium* ser. *Coriacea* (Barneby & Grimes 1996). The generic concept of *Macrosamanea* was expanded in 1940 by Kleinhoonte to include an albizioid taxon, *Mac. pedicellaris* (DC.) Kleinh. (=*Balizia pedicellaris* (DC.) Barneby & J.W.Grimes). It was in relation to this taxon that *Macrosamanea* was synonymised under *Albizia* by Nielsen (Barneby & Grimes 1996). *Macrosamanea* sensu Barneby and Grimes (1996) is therefore equivalent in generic concept to 'Genus D' of Nielsen (1981a), with minor adjustments.

The large predominantly neotropical genus *Calliandra* has shrunk since Nielsen's 1981 classification, with two new genera being erected from it: *Viguieranthus* Villiers, primarily found in Madagascar (see 'Other regions' below); and *Zapoteca* from the Neotropics. Palynological studies of *Calliandra* indicated that two clear groups of taxa existed: one with 16-grained polyads (as found in the majority of the Ingeae) and the other with 8-grained polyads. A number of other characters can also be used to distinguish between these two groups including, characteristics of the leaflets, inflorescence, stigmas, legume, seedlings and number of chromosomes (Hernández 1986). As a result, the taxa that were formerly placed in *Calliandra* ser. *Laetevirntes*, with 16-grained polyads, were transferred to the new genus *Zapoteca* (Hernández 1986). The other major development was the subdivision of *Calliandra* into five sections and 14 series by Barneby (1998).

Three new genera have been described from *Havardia* sensu Nielsen (Barneby & Grimes 1996), each comprising three species: *Ebenopsis*, *Painteria* and *Sphinga*. *Ebenopsis* was defined by its unique pod, which is massive, ligneous, and internally septate with "obese reddish seeds". *Painteria* was "feebly distinguished from *Havardia* by tougher-walled, falcately or further recurved pods, and by straight or sinuous but not distally sigmoid seed funicles" (Barneby & Grimes 1996: 179). Members of the third genus, *Sphinga*, have been considered closely related since Bentham (1875) and were distinguished from *Havardia* because of their "greatly elongated perianth, with long, silky corolla expanding at nightfall" (Barneby & Grimes 1996). Phylogenetic analysis of these four genera — *Ebenopsis*, *Havardia*, *Painteria*, and *Sphinga* — and *Pithecellobium*, which appear to form a natural morphological group, revealed that *Sphinga* and *Havardia* are sister taxa and the three other genera form a clade, with *Painteria* and *Pithecellobium* sister taxa, and *Ebenopsis* related to them (Barneby & Grimes 1996).

Barneby and Grimes' (1997) concept of *Pithecellobium sens. str.* does not appear to differ greatly from that of Nielsen (1981a). However, they established a new genus, *Leucochloron*, for *Pithecellobium incuriale*, which Nielsen (1981a) left as affinity unknown, and three related species (Barneby & Grimes 1996). *Leucochloron* is hypothesised to be closely related to *Chloroleucon* but differs in characteristics of the axillary branchlets, pod and seed.

Blanchetiodendron is another newly described neotropical genus; it has previously been placed in *Pithecellobium*, as well as *Enterolobium* and *Albizia* (Barneby & Grimes 1996). The genus was defined by characteristics of the inflorescence, pod and seed, and is clearly related to two groups of taxa: *Leucochloron* and *Chloroleucon*, and *Albizia* sect. *Arthrosamanea*. However, it is morphologically isolated from both (Barneby & Grimes 1996).

The last new genus of Ingeae that was described from the neotropics post Nielsen 1981 is *Guinetia*; it was discovered in Mexico in 1968 but not described until 30 years later (Rico Arce *et al.* 1999). It is a monotypic genus and has characteristics of both the *Chloroleucon* and *Inga* alliances (see below), but does not match any taxon within those groups.

The phylogenetic relationships, of tribe Ingeae, resolved by Grimes (1995) was the basis of the informal grouping of genera into alliances by Barneby and Grimes (1996). For the neotropical taxa, five alliances were

identified and four genera were left as affinity unknown until they can be comprehensively analysed: *Albizia*, *Enterolobium*, *Cedrelinga* and *Lysiloma*. The genera from other geographic regions, with the exception of *Archidendron*, were not placed into alliances. The alliances identified by Barneby and Grimes (1996), shown in Table 2, were: the *Abarema*–alliance including, *Abarema*, *Hydrochorea* and *Balizia*; the *Chloroleucon*–alliance including, *Blanchetiodendron*, *Chloroleucon* and *Leucochloron*; the *Inga*–alliance including, *Archidendron*, *Calliandra*, *Cojoba*, *Inga*, *Macrosamanea*, *Zapoteca* and *Zygia* (including *Marmaroxylon*); the *Samanea*–alliance

Table 2. Alliance composition comparison table. The genera of each alliance are listed as per the system of Barneby and Grimes (1996), with changes from Grimes (1999) incorporated[B], and compared to the system suggested by Lewis and Rico (2005).

Alliance	Barneby & Grimes (1996)	Lewis & Rico (2005)
Aborema–alliance	*Aboremo*	*Aboremo*
	Hydrochoreo	*Hydrochareo*
	Bolizia[A]	*Pororchidendron*
Chloroleucon–alliance	*Blonchetiodendron*	*Blonchetiodendron*
	Chlaraleucan	*Cothormion*
	Leucochloron	*Chloroleucon*
	Lysilomo[B]	*Leucochloron*
		Thoilentodopsis[C]
Inga–alliance	*Archidendron*	*Archidendron*
	Calliandro	*Colliondra*
	Cothormion[B]	*Cedrelingo*
	Cojobo	*Guinetio*[C]
	Inga	*Cojoba*
	Mocrosomonea	*Inga*
	Zopoteco	*Mocrosomoneo*
	Zygio (incl. Marmaraxylon)	*Mormoroxylan*
		Viguieranthus[C]
		Zygio
Somoneo–alliance	*Albizio lebbeck*[B]	
	Hesperolbizio	*Hesperolbizio*
	Somoneo	*Somoneo*
	Pseudosomoneo	*Pseudosomaneo*
Pithecellobium–alliance	*Ebenapsis*	*Ebenopsis*
	Hovordio	*Hovordio*
	Sphingo	*Sphinga*
	Pointerio	*Pointerio*
	Pithecellobium	*Pithecellobium*
Unplaced genera	*Albizio*	*Albizio*
	Cedrelingo	*Enterolobium*
	Enterolobium	*Lysilomo*

[A] *Balizia* was not recognised as a genus by Lewis and Rico (2005).
[B] taxa were placed into alliance after the analysis of Grimes (1999).
[C] taxa were described/reinstated after the revision of Barneby and Grimes (1996).

including, *Hesperalbizia*, *Samanea* and *Pseudosamanea*; and the *Pithecellobium*–alliance including, *Ebenopsis*, *Havardia*, *Sphinga*, *Painteria*, and *Pithecellobium*.

Grimes (1999) later published an updated phylogeny of the Ingeae, with revised morphological characters and previously missing data included. Some Old World taxa were represented in this phylogeny, however, no comprehensive cladistic analysis of the Old World genera was presented. The revisions resulted in several changes to the alliances (Table 2): *Cathormion* was placed in the *Inga*–alliance; the relationships between genera of the *Abarema*–alliance were now considered unresolved (previously *Abarema* was considered the derived genus of this alliance); *Albizia lebbeck* was included in the *Samanea*–alliance because of its similarity to *Samanea saman*; and the *Chloroleucon*–alliance now includes *Lysiloma*, which was previously unplaced and poorly studied in 1995.

Other regions

Genera of the Ingeae are also native to Africa, Madagascar and the Middle East and extend into Mainland Asia (Lewis & Rico Arce 2005). Ingeae in these regions have not been as extensively revised as for the Neotropics and SE Asia, the Pacific Islands and Australia, however, some important taxonomic changes have occurred in the past 25 years. The two main changes have been the transfer of *Faidherbia* A.Chev. to the tribe Ingeae from Acacieae, and the description of a new genus *Viguieranthus*.

In the first volume of 'Advances in Legume Systematics', when Nielsen reviewed the Ingeae, Vassal (1981) provided a revision of the related tribe Acacieae, recognising two genera in the tribe: *Acacia* and the monotypic *Faidherbia*. These genera were differentiated by a character of pollen tectum, and the tribe was distinguished from the Ingeae by stamens being free and not united into a tube, although, exceptions were known (see 'What are the Ingeae?' above). *Faidherbia* is one of these exceptions with "stamen filaments shortly connate basally" (Vassal 1981: 170). Vassal (1981) considered it more appropriate to include *Faidherbia* in tribe Acacieae, while Polhill (1994) later transferred it to the Ingeae. Recent phylogenetic analyses of the Ingeae (Luckow *et al.* 2003; Miller *et al.* 2003), support the transfer suggested by Polhill with *Faidherbia* placed as the sister taxon to *Zapoteca* (Ingeae).

The second major change to Ingioid taxa outside SE Asia–Pacific Islands–Australia and the Neotropics has been the segregation of *Viguieranthus* from *Calliandra* (Villiers 2002). *Viguieranthus* includes 23 species from Asia and Madagascar, differentiated from *Calliandra* by the possession of leaves with only a single pair of pinnae and inflorescences with homomorphic flowers (Villiers 2002). Hernández (1986) also noted that species of *Calliandra* from Madagascar and India were palynologically dissimilar to the remainder of the genus. However, Villiers only made combinations for the 18 Madagascan taxa when describing the genus, despite noting that it is also found in Asia. Only three taxa have been ascribed to *Calliandra* in Asia, so presumably these are the Asian *Viguieranthus* mentioned by Villiers (2002); formal nomenclatural combinations have yet to be made. The other two species ascribed to *Viguieranthus* have been suggested to be the "two rejected African calliandras", "highlighting the poor state of knowledge of generic limits within the Old World calliandras" (Lewis & Rico Arce 2005: 199).

This poor state of knowledge is not just limited to the genus *Calliandra*. The African taxa that have been ascribed to *Cathormion*, but currently recognised as *Albizia* (Nielsen 1981a) require revision. Barneby and Grimes (1996: 247) questioned whether the African *Cathormion* is congeneric with the Asiatic *Cathormion*, however, this has yet to be tested.

The Ingeae from Madagascar have recently been revised by Villiers (2002) for 'The Leguminosae of Madagascar'. In addition to the description of *Viguieranthus* (see above), it is interesting to note that Villiers' adopted the broad concept of *Albizia* sensu Nielsen, with *Albizia saman* (= *Samanea saman*) recognised as one of the 30 species of *Albizia* (Villiers 2002).

Ingeae in familial classifications

These regional revisions have provided the taxonomic framework for the Ingeae in recent familial classifications (Polhill 1994; Lewis & Rico Arce 2005). In Polhill's 1994 classification of the family Leguminosae, most of the discussion related to the subfamily Papilionoideae, however, the synopsis of legume genera included information on all subfamilies. The classification of the tribe Ingeae incorporated the work by Nielsen and

Nielsen *et al.* (1981a,b; 1983; 1983; 1984a,b; 1985; 1992) but Polhill (1994) has doubts over the characterisation of some New World genera, which have since been revised by Barneby and Grimes (see 'The Neotropics' above). Polhill (1994) recognised 25 genera in the Ingeae (Table 1), including *Faidherbia*.

The next, and most recent, classification of the family Leguminosae was published in 2005 ('Legumes of the World', edited by Lewis *et al.* 2005). The Ingeae treatment was compiled by Lewis and Rico, which brought together information from all of the regional revisions (above), presenting a synopsis of each genus with photos and descriptions. Most of the generic changes from the regional revisions were adopted, however, some were not: *Marmaroxylon* was recognised as a separate genus, although Barneby and Grimes (1996) had treated it as part of *Zygia*; and *Balizia* was not considered a separate genus from *Albizia* (Rico Arce 1999).

A diagram of hypothesised relationships of genera in the Ingeae was also included. This largely corresponded to the alliances of Barneby and Grimes (1996) but included some changes based on the molecular phylogenetic study of Luckow *et al.* (2003; Table 2). Lewis and Rico (2005) also created an Old World group to accommodate most taxa restricted to the SE Asian, Pacific Island and Australian region, excluding *Archidendron* and *Pararchidendron*. The *Pithecellobium*– and *Samanea*–alliances remain as described in Barneby and Grimes (1996) but Lewis and Rico (2005) did not mention the incorporation of *Albizia lebbeck* into *Samanea*–alliance suggested by Grimes (1999). There have been some alterations to the other three alliances (Table 2).

As *Balizia* was not recognised by Lewis and Rico (2005), it was not acknowledged in the *Abarema*–alliance. The other change to the *Abarema*–alliance was the inclusion of the Old World genus *Pararchidendron* (Table 2). No justification for its inclusion was provided and this relationship was not suggested in Barneby and Grimes (1996) nor the phylogeny of Luckow *et al.* (2003).

The genera *Cathormion* and *Thailentadopsis* were included in the *Chloroleucon*–alliance by Lewis and Rico (2005), although again, it is not clear why. Presumably *Thailentadopsis* was added because of its suggested relationship to *Cathormion* (Lewis & Schrire 2003), but Grimes (1999) placed *Cathormion* in the *Inga*–alliance, not the *Chloroleucon*–alliance. In the molecular phylogeny of Luckow *et al.* (2003) *Cathormion* is placed next to *Chloroleucon* on the tree, however, they are both in an unresolved polytomy, with numerous other taxa, and therefore not necessarily closely related.

The *Inga*–alliance of Lewis and Rico (2005) has changed the most from its original concept (Table 2). Based on results of Luckow *et al.* (2003), Lewis and Rico removed *Zapoteca* from the *Inga*–alliance and placed it, with *Faidherbia*, as sister to the rest of the tribe. Four genera have been added to the *Inga*–alliance. *Marmaroxylon* and *Viguieranthus* were recognised from genera already included in the *Inga*–alliance and the affinities of the newly described taxon, *Guinetia*, also came from within the *Inga*–alliance. The inclusion of *Cedrelinga*, however, is not well justified. Presumably it was placed in the *Inga*–alliance because it was the sister to *Calliandra* in the phylogeny of Luckow *et al.* (2003); however, the support for this relationship is extremely weak (35% bootstrap support).

Phylogenetic relationships of the Ingeae

Morphological phylogenies

Three papers attempting to resolve the relationships of the genera of the Ingeae, based on morphological data, were published in the 1990s (Chappill & Maslin 1995; Grimes 1995; Grimes 1999). The relationships of the ingioid genera in each of the analyses are not especially congruent, but this may be due to different generic sampling and the use of different characters. All of these phylogenies, however, are in agreement that the Ingeae is not monophyletic, with the different clades of Acacieae nested within the tribe Ingeae (Chappill & Maslin 1995; Grimes 1995; Grimes 1999).

Chappill and Maslin (1995) focused on the relationships within the Acacieae yet also investigated its relationships to the other tribes of the subfamily, based on characters of morphology, pollen, chemistry and anatomy. All infra-generic groups of the Acacieae were represented along with at least one exemplar from each other tribe; 24 genera of the Ingeae were sampled. As a result, some relationships between genera of the Ingeae were hypothesised but not discussed in detail.

The phylogeny of Grimes (1995) primarily focused on the New World *Pithecellobium*–complex using macromorphological, developmental, anatomical and pollen characters; this analysis formed the basis of the alliances described in the Barneby and Grimes (1996; 1997) and Barneby (1998) revisions. Four years later Grimes (1999) published another phylogeny of the Ingeae based on a modified data set. The results were generally congruent with his 1995 analysis but some modifications to the originally proposed alliances of the Ingeae were required (discussed above).

Molecular phylogenies

Members of the tribe Ingeae have also been included in various molecular phylogenetic studies; all of these have been based on sequences of chloroplast DNA (cpDNA) regions. However, two studies utilised a region of nuclear DNA (nDNA) in conjunction with a cpDNA region (H3-D, Miller & Bayer 2000; ITS, Richardson *et al.* 2001). With a few exceptions, these molecular phylogenetic studies included too few representatives (genera or species) to make meaningful inferences about the relationships within the tribe Ingeae (Dayanandan *et al.* 1997; Clarke

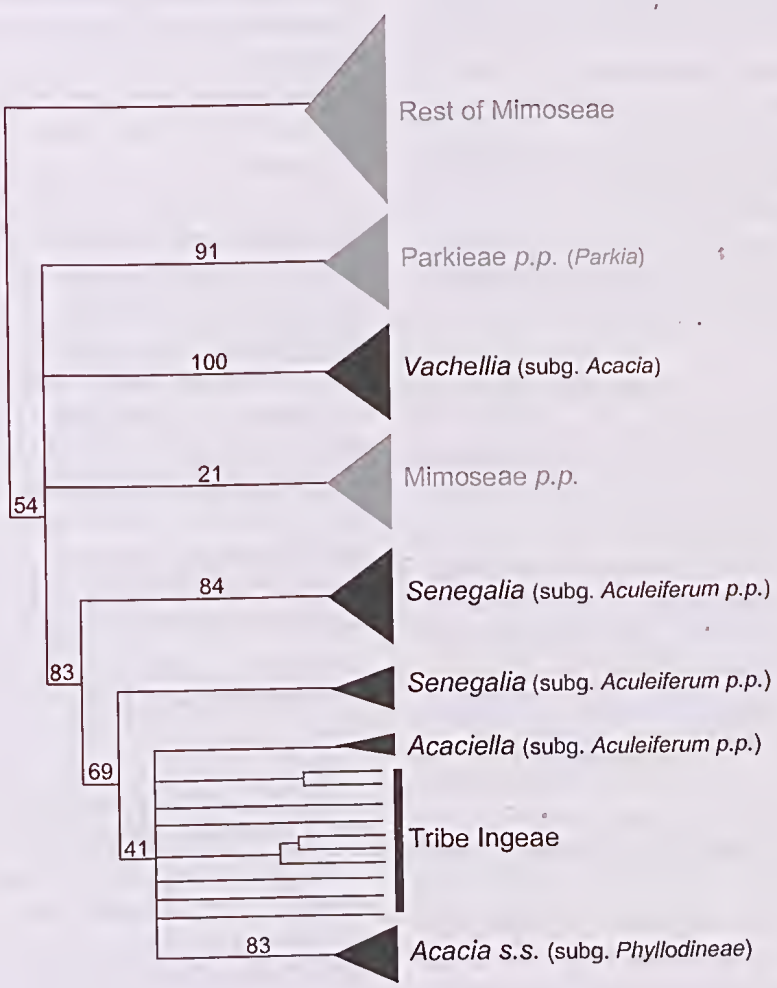

Figure 2. Relationships between members of the tribe Acacieae and Ingeae (adapted from Luckow *et al.* 2003). This is a summary phylogeny of the Mimosoideae, based on cpDNA data, of Luckow et al. (2003). Triangles represent a clade, while numbers above the node represent bootstrap values for that clade node. Clades of tribes Mimoseae and Parkieae are in grey; tribe Acacieae in black and tribe Ingeae.

et al. 2000; Luckow *et al.* 2000; Miller & Bayer 2000; Robinson & Harris 2000; Kajita *et al.* 2001; Miller & Bayer 2003; Wojciechowski *et al.* 2004; Lavin *et al.* 2005). More detailed and densely sampled molecular phylogenetic studies of the Ingeae are currently underway (Brown *et al.*, submitted).

The studies that have sampled the most Ingeae were focused on the phylogenetic relationships of the subfamily Mimosoideae (32 species/16 genera, Luckow *et al.* 2003) and the tribes Acacieae and Ingeae (21 species/15 genera, Miller *et al.* 2003). The results of these two studies were congruent, which is to be expected as they sequenced the same regions of cpDNA (*trn*K, *mat*K, *trn*L intron and *trn*L-*trn*F spacer; Miller *et al.* (2003) also sequenced the *psb*A-*trn*H spacer). The tribe Ingeae was placed in an unresolved polytomy, along with a monophyletic *Acacia sens. str.* (formerly *Acacia* subg. *Phyllodineae*) and two species of *Acaciella* (Fig. 2; Luckow *et al.* 2003; Miller *et al.* 2003): *Ac. boliviana* and *Ac. visco*. This polytomy may be a result of limited sampling or alternatively there may be insufficient informative characters in these DNA loci to resolve these relationships.

Relationships between members of the Ingeae were generally unresolved, however, some inferences can be made. Six genera were found to be monophyletic: *Calliandra*, *Ebenopsis*, *Enterolobium*, *Havardia*, *Lysiloma* and *Zapoteca*. The sampling of each genus was very limited, with most including only two species, although, three species (c. 38% of the genus) were included for *Lysiloma* and five species (c. 4% of the genus) for *Calliandra*. *Albizia* was the only genus, sampled for more than one species that was identified as polyphyletic. *Inga* was confirmed as monophyletic (Richardson *et al.* 2001), with 44 species (c. 15% of the genus) sampled for two regions of DNA (ITS and *trn*L–*trn*F).

In both analyses, *Ebenopsis* and *Havardia* formed a clade, as did *Faidherbia* and *Zapoteca*. An additional node was supported in the analysis of Miller *et al.* (2003), although the bootstrap value was low (56%): grouping *Albizia kalkora* and *Cat. umbellatum* with the monophyletic *Enterolobium*. A similar relationship was found with the H3-D nDNA region (Miller & Bayer 2000).

What is next for the Ingeae?

Although there have been considerable advances in the systematics of the Ingeae over the past 25 years, we have only just started to scratch the surface of this large, diverse and important group of legumes. Many of the difficulties and challenges that impede on the taxonomy and classification of the Ingeae, such as, getting to know large numbers of taxa over a broad geographical area and the resultant reliance on geographically focused studies which often lack monographic synthesis, also hinder the systematics of other large pantropical groups.

There are still many questions unanswered in relation to the systematics of the Ingeae, including defining the tribal limits. Should the tribe Ingeae be merged with the tribe Acacieae or should it be split up into several supergeneric taxa? With a revision of tribal classification of the Mimosoideae imminent (Luckow 2005), it is vital that we have a better understanding of the phylogenetic relationships within the currently circumscribed Ingeae. Despite an increase in phylogenetic analyses including taxa of tribe Ingeae in recent years, much remains to be done. The most comprehensive morphological analyses of the tribe to date (Grimes 1995; 1999), present only a preliminary and partially resolved hypothesis of sister group relationships for the tribe with many of the Old World taxa not well sampled (Grimes 1995; Hughes 1997). While in molecular phylogenetic studies, which can provide statistical support for the monophyly of genera and higher level grouping, sampling of the Ingeae have included only half of the 36 currently recognised genera and less than 5% of all Ingeae species.

Current data, based on limited taxon and character sampling, indicate *Acacia sens. str.* (formerly *Acacia* subgenus *Phyllodineae*) is nested within a paraphyletic Ingeae (Fig. 2) and is distantly related to other groups of tribe Acacieae. By advancing our knowledge of the Ingeae, we will also improve understanding of the evolutionary history of related genera, including *Acacia sens. str.*, which is the largest genus of woody, flowering plants in Australia and an ecologically significant group, being the dominant tree or shrub in many ecosystems. Uncovering the phylogeny of the Ingeae will assist in identifying the closest relative of *Acacia sens. str.*, therefore improving the classification of *Acacia sens. str.* for all end-users. However, as well as molecular phylogenies, diagnostic morphological characters

need to be identified that can be used for defining taxa that are meaningful for the broader community and end-users of taxonomic information. Many potential morphological characters in the Ingeae have been identified through monographic work, and careful interpretation of these will enhance molecular studies currently under way and in the future.

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Leaf ontogeny and morphology in *Acacia* Mill. (Mimosaceae)

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Introduction

Leaves are the primary organs of photosynthesis in most higher plants. Despite their common function they display a spectacular diversity of form and structure. For several centuries botanists have attempted to define and explain the wide variety of leaf shape and size found within and between individuals. Various factors have been identified that influence variation within individuals: external factors such as mineral nutrition, light intensity and day length, and internal factors such as plant physiological age and the position on the plant at which the leaf arises (Ashby 1948). Developmental processes must mediate these influences, and molecular biology is just beginning to grasp the complexity of the interactions involved (e.g. Tsiantis & Hay 2003; Fleming 2005; Tsukaya 2006).

The classical model of plant morphology divides plants' bodies into four discrete types of organs. These are the phyllome (leaf), caulome (stem), rhizome (root) and trichome (numerous sources, see Rutishauser & Sattler 1985). All plant structures are considered to be modified versions of these basic units (e.g. flower petals are modified leaves). Leaves, as phyllomes, differ from other classical plant structures in several ways. They are formed as lateral organs from the shoot apical meristem and generally exhibit determinate growth and dorsiventral symmetry.

Leaves can be classified into two basic forms: simple with a single blade region, or compound with multiple connected blade regions. Compound leaves are widespread and are believed to have arisen numerous times in angiosperms with multiple reversions to simple leaves (Champagne & Sinha 2004). Two hypotheses have been proposed to explain the homology of compound leaves, and have been debated for fifty years. The first follows the precepts of classical morphology and suggests that the whole compound leaf is the equivalent of a simple leaf, with leaflets arising as subdivisions of the blade (e.g. Troll 1939). In this view toothed, lobed, pinnate and bipinnate leaves represent increasing levels of dissection. The second hypothesis of compound leaf homology equates each individual leaflet to a simple leaf and the entire structure as a 'partial shoot' (Sattler 1992).

Abstract

The recently redefined genus *Acacia* consists of more than 1000 species, nearly all of which are endemic to Australia. *Acacia* foliage is highly variable and all species exhibit heteroblastic leaf development to some extent as seedlings, with a typical progression from pinnate to bipinnate leaves in the first few seedling nodes followed in most species by the transition to phyllodes. Although phyllodes occur in several plant families, the *Acacia* phyllode is unique and its structure, development and the genetic processes involved in its formation are not well understood. Despite its significance for classification, the developmental homology of this character remains uncertain. Modern microscopy and molecular genetic studies into leaf morphology and development suggest the concepts of process morphology may allow a different way of interpreting the foliage changes exhibited by *Acacia* species.

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Early studies of plant development focused on identifying 'initial' cells that were the progenitors of certain cell types, tissues and organs, and using this knowledge to reveal structural homology. This "zoocentric" outlook viewed cells as gaining a certain identity or fate that was passed on to all daughter cells. The variability of plants confounded attempts to identify these 'initials' (e.g. Boke 1940 [*Acacia* Mill.]; Pray 1957 [3 monocot genera]; Denne 1966 [*Trifolium* L.]). Plant cells have greater general potency and thus their cellular identities do not become so fixed during ontogeny as in animals, but rely more upon hormone gradients across tissues and intercellular signalling.

The occurrence of structures that could not be satisfactorily categorised under the classical model led to the concept of continuum morphology. This model describes a continuous field of possible structures in which the classical forms are the extreme types, between which occur a range of intermediate structures (Sattler & Jeune 1992; Sattler 1996). The 'partial shoot' theory suggests that the compound leaf is an intermediate structure somewhere in the continuum between a leaf and a shoot (for another example of continuum morphology using *Acacia* see Sattler *et al.* 1988). This also implies a combination of developmental processes particular to each type of organ, in this case the dorsiventral symmetry and determinate growth of leaves and the stem-like production of lateral organs (Sattler 1992). Considering organs as combinations of processes, and the continuum of plant form as a continuum of process combinations is the essence of process morphology. This concept allows direct comparison of the development of differing organs and a deeper understanding of plant growth. In order to understand leaf form and evolution, including the phyllode, we must identify the processes involved in leaf development, and the differences between simple and compound leaves are fundamental to this subject.

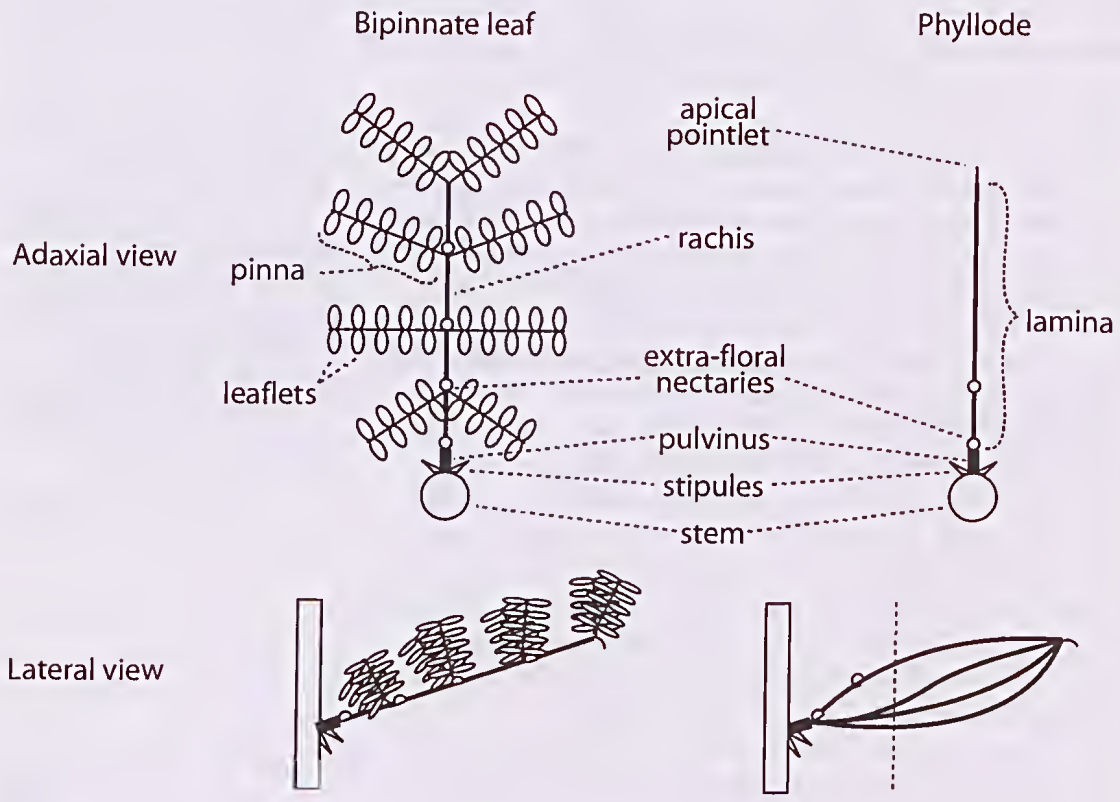

Figure 1. Typical external morphology of bipinnate leaves and phyllodes in the genus *Acacia*.

Acacia foliage and the history of the phyllode

Acacia is the most speciose genus of vascular plants in Australia and has a complex taxonomic history. Vegetative characters have had a prominent role in the infra-generic classification due to the similarity of floral features throughout the genus. *Acacia* foliage is highly variable and all species exhibit heteroblastic leaf development to some extent as seedlings. A typical progression goes from pinnate to bipinnate leaves in the first few seedling nodes followed in most species by the transition to phyllodes. Of the currently described and accepted species of *Acacia*, approximately 70 have bipinnate compound leaves at maturity and more than 900 have phyllodes (Maslin 2003).

Phyllodes and compound leaves of *Acacia* share several common features (Fig. 1) with rare exceptions. They both bear an axillary bud, have stipules that are usually caducous, and at least one extra-floral nectary located on the adaxial edge of the rachis or phyllode. They have a small apical pointlet at the tip, and a pulvinus at the base, but unlike other Mimosoid genera the pulvini of *Acacia* appear to be incapable of seismonastic (response to touch) and nyctinastic (response to light intensity) movements (Wilkinson 1983). While the compound leaf includes a petiole, rachis, pinnae and leaflets, the phyllode consists of the pulvinus and a photosynthetic zone, loosely termed the lamina. The lamina is vertically flattened in most species, although some are terete, horizontally flattened or reduced to scales. In some species the pulvinus is absent, in which case the phyllodes are decurrent. Two striking anatomical features of the phyllode are the isobilateral lamina symmetry and the opposing pairs of vascular bundles that comprise the major veins (Fig. 2).

The homology of the *Acacia* phyllode has caused much debate among morphologists and taxonomists in the last two centuries. Willdenow (1806), in his

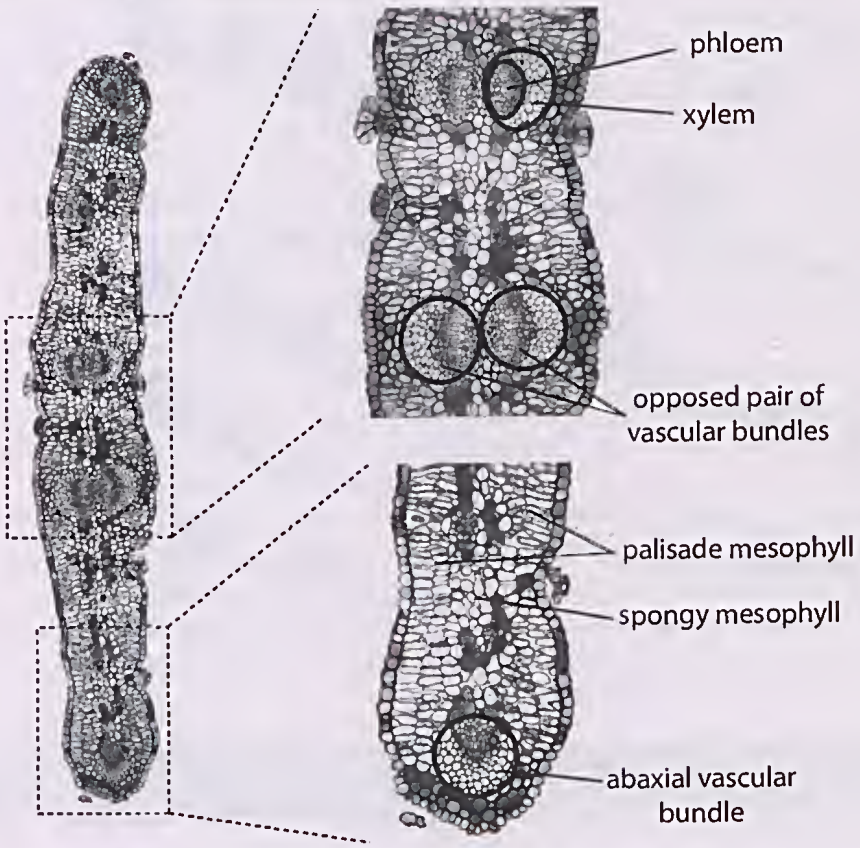

Figure 2. Transverse section of a phyllode (dotted line through phyllode on Fig. 1) showing significant points of anatomy.

classification of *Acacia* based on foliage types, referred to it as a 'simple leaf'. The term "phyllodium" appears to originate from Candolle (1813), literally meaning 'like a leaf', implying that it fulfilled the functions of a leaf yet was not a leaf, nor was it a photosynthetic stem (cladode, phylloclade or cladophyll). A variety of transitional forms occur between the seedling bipinnate leaves and mature phyllodes present in the phyllodinous Australian acacias (Fig. 3a). Reinke (1897) interpreted these as indicating that the mature structure was in fact derived from the petiole of a pinnate leaf. In his discussion of plant vegetative structures, Goebel (1905) stressed the importance of the arrested leaf primordium to the concept of a phyllode; i.e. if an apparently primitive vegetative structure is a phyllode, and so derived and reduced from a true leaf, there must be a remnant arrested leaf primordium at its apex. In Goebel's view, without an arrested leaf primordium the structure must either be a true leaf or a primitive enation. Some of the earliest work on *Acacia* phyllodes states that they are completely lacking an arrested leaf primordium (Hildebrand 1875) but Goebel (1884; 1905) and Mann (1894) considered this to be incorrect, and that what appeared to be a leaf primordium could always be observed at the apical tip of a developing phyllode. This structure was variously named the arrested true leaf primordium or the terminal seta, depending on the author's opinion of its homology. Many settled upon the neutral term 'apical pointlet', simply referring to its location and appearance, rather than any implication of origin.

Various publications from the 1870s to the 1970s expressed two different views concerning the precise homology of the *Acacia* phyllode and the apical pointlet

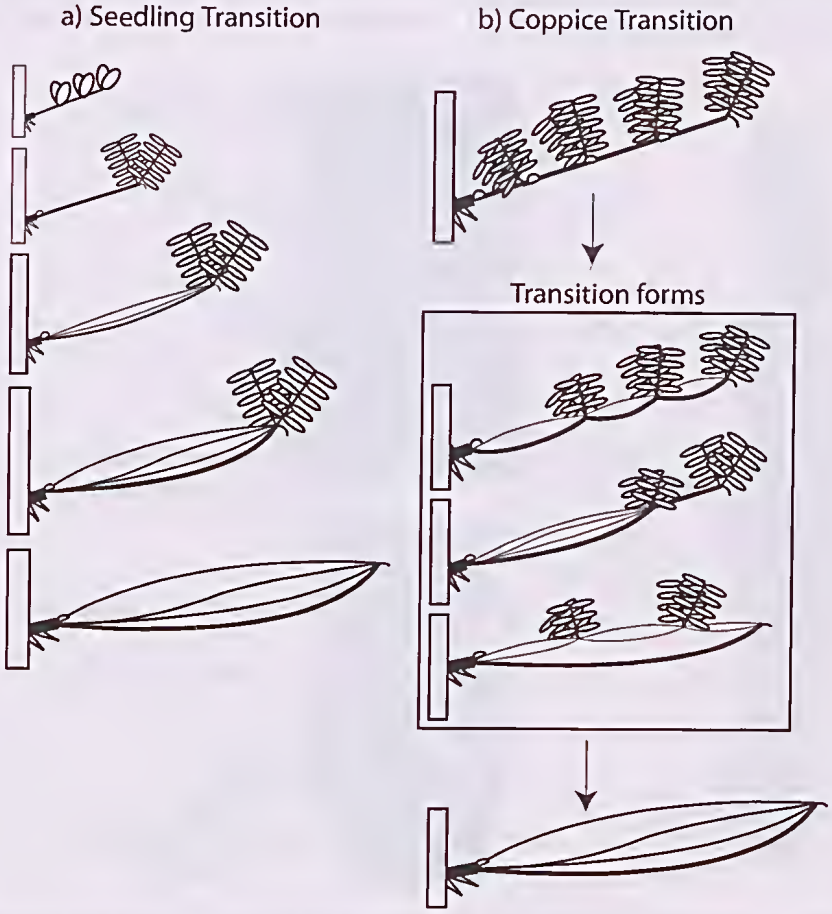

Figure 3. a) Typical heteroblastic leaf progression of an *Acacia* seedling; **b)** typical heteroblastic leaf progression in *Acacia* coppice reversion shoots.

at its tip. Mann (1894), Reinke (1897), Arber (1918), Peters (1925), Troll (1939) and Vassal (1970) regarded the phyllode as having developed from only the petiole of a bipinnate leaf. Bentham (1875), Preston (1902), Fletcher (1920) and Catalano (1934) thought that the petiole and the rachis were involved in the formation of the phyllode. Bentham (1864, 1875) and Goebel (1895, 1905, 1928, 1932) supported both hypotheses at different times. Goebel, Mann and Troll considered the apical pointlet of the phyllode equivalent to the whole lamina of a foliage leaf, and Catalano thought that the apical pointlet must be an aborted terminal leaflet. All these conclusions were predominantly based upon external form and development. The petiole hypothesis arose primarily from observations of seedling transitions that display a uniform development of phyllode lamina below the pinnae. It was called into question by work on coppice reversion shoots with much more irregular lamina development (Fig. 3b), which suggested the petiole-rachis homology. Arber (1918) differed from this trend and supported the petiolar hypothesis based on the organization of the mature vasculature bundles, noting the similarity to monocotyledonous leaves and dicotyledonous leaf bases and petioles. Despite exhaustive debate on this topic, both hypotheses remained in common usage. This issue is further complicated because although it is clear that in English the petiole refers only to the stem of a leaf, one of the earliest uses of the term is in an early German herbal by Leonhart Fuchs (1541, Rutishauser, R. pers. comm.) where he explicitly includes the bipinnate leaf rachis in its definition.

Outside the genus *Acacia*, the term 'phyllode' has been applied to a number of other species with leaves that consist only of tissues derived from the petiole. Troll (1939) applied the term 'phyllode' to species from the Crassulaceae, Apiaceae and Oxalidaceae, and Arber (1918) proposed the phyllode theory of monocot leaf origin. Neither of these proposals gained significant support and today the term is generally restricted to acacias.

Boke (1940) performed the first histogenetic study of phyllode morphology using *Acacia longifolia* (Andrews) Willd. He attempted to identify cell lineages and discrete meristems that determined the form of adult phyllodes with limited success. In the shoot apical meristem he found the layers of tunica to be variable and not always distinct from the corpus, nor did they have identifiable initials. He also failed to find initial cells for leaf primodia in any layer of the tunica, instead identifying multiple divisions in many layers occurring almost simultaneously. These observations lead him to suggest that a more dynamic view of the morphology and terms was necessary.

The majority of Boke's work consisted of detailed observations of cell division in developing phyllodes. He described a leaf sub-apical meristem that produced the early lengthening of the phyllode primordium, and the early maturation of the abaxial tissues combined with the appearance of an adaxial meristem. He described how this meristem produced the vertically expanded phyllode. In explaining the origin of this meristem Boke referred to much less active 'adaxial meristems' he considered similar in the petioles and leaf axes of non-phyllodinous acacias and other angiosperms. Boke considered the change from bipinnate foliage to phyllodes to be the loss of the leaf blade meristem and/or leaflet primordia, and the precocious action of a discrete adaxial meristem. With this idea established, he did not examine other *Acacia* leaf forms in depth, but rather applied the idea to explain the leaf morphology of *A. dealbata* Link (bipinnate; was then *A. decurrens* var. *dealbata* (Link) F.Muell. ex Maiden) and *A. melanoxylon* R.Br. (phyllodinous with slow transition). He described the range of leaf forms as variations in the 'strength' of each meristem. Bipinnate leaves had 'strong' leaflet primordia; phyllodes had a strong adaxial meristem; and intermediates had moderate leaflet primordium 'strength', producing a few pinnae and moderate adaxial meristem 'strength' causing expansion of the axis below and sometimes between the pinnae. He concluded that

Table 1. Hypotheses of phyllode homology in *Acacia*.

Bipinnate leaf structure	Petiole hypothesis	Rachis hypothesis	Lamina hypothesis
Petiole	phyllode blade	phyllode blade	greatly reduced
Rachis	apical pointlet	phyllode blade	phyllode blade
Pinnae & Leaflets	apical pointlet	absent	phyllode blade

the phyllode was the equivalent of the petiole-rachis of a pinnate foliage leaf.

Boke observed the presence of an apical pointlet not only on the phyllodes, but also on the pinnate and transition leaves of this species, on the bipinnate leaves of *A. decurrens* Willd., and on all foliar types in *A. melanoxylon*. Boke (1940) concluded that as an apical pointlet occurred in pinnate, bipinnate, transition and phyllodinous leaves, it could not represent an aborted lamina. It was simply the physical apex, or at most an abortive terminal leaflet. Argument on this topic appears to have been suspended for many years, although the petiole hypothesis persisted in texts (McLuckie & McKee 1954; Debenham 1971).

Boke's study showed detailed development of a phyllode for the first time, rather than simply drawing conclusions from adult structures. He clarified that phyllode expansion was adaxial, not in both directions as previously thought; however his preconceptions of discrete meristems caused him to overlook the possibility of a link between what he called the increasing strength of the adaxial meristem and decreasing strength of the leaflet primordia, and the fact that both meristems occurred on the adaxial surface. This was due to the lack of comparison to juvenile pinnate and bipinnate leaf development, a problem that was only remedied 40 years later by Donald Kaplan.

Kaplan (1975) carried out the first detailed investigation of the development of bipinnate *Acacia* leaves using coppice reversion shoots of *A. melanoxylon*. He discovered that the petiole was actually produced by late intercalary divisions, after the formation of the rest of the leaf. He detected no sign of lamina suppression in favour of petiole expansion; rather he observed a reduction of late intercalary divisions – actual suppression of the petiole such that it is almost absent in mature phyllodes. He concluded that the phyllode is the positional homologue of the bipinnate leaf lamina. This led Kaplan (1980) to perform the first comparative developmental analysis of *Acacia* foliage in an attempt to reconcile the disparate interpretations of this structure. He observed that previous studies of phyllode ontogeny were either done at a superficial organogenetic level or were not sufficiently comparative to determine structural equivalences. He examined the growth and development of seedling leaves to mature foliage in four species (*A. longifolia*, *A. pravissima* F.Muell, *A. verticillata* Willd. and *A. melanoxylon*) using transverse and radial longitudinal sections. Through observations of the timing and location of growth and differentiation he identified the stages and processes involved in formation of pinnate, bipinnate and transition leaves as well as phyllodes.

Kaplan identified two separate and seemingly independent processes occurring in the heteroblastic leaf development of acacias. The first and most obvious was the change from dissected to simple blade morphology. The second change was the progressive increase in lamina length and decrease in petiole length. The dramatic shift to simple blade form generally obscured the second trend. Kaplan proposed that this was largely responsible for the conflicting opinions of phyllode homology. In studies using coppice reversion shoots the second trend (increase in lamina length/decrease in petiole) is well advanced; reduction in dissection is the only transition occurring and the lamina homology of the phyllode has been apparent. Studies of seedling transition leaves observed both changes occurring simultaneously and thus the phyllode appeared to be in the position of the petiole as the number of pinnae was reduced and the rachis expanded.

Kaplan and Boke similarly concluded that the phyllode was the equivalent of the bipinnate lamina, but had very different ideas about the development of the structure. Boke believed that the different foliage forms were controlled by the switching on and off of discrete meristems. Kaplan regards the change from dissected to simple lamina to be a congenital suppression of the pinnae primordia, but the vertical mode of growth to be the same in the two types of foliage (pinnae arising adaxially, phyllodes expanding adaxially), hence his use of the term 'positionally equivalent'. It is the difference between viewing form structurally (meristem type A produces organ type A, meristem B produces organ B), and interpreting it by the processes which create and maintain it (a background of vertical expansion, with an overlaying process of varying levels of dissection).

The concepts of the rachis and petiole of the bipinnate acacia leaf, and their respective contributions to the development of the phyllode, have been the

sticking point of morphological argument about the phyllode for more than 100 years. The differences between the petiole and the rachis are few. Although the anatomy has not been adequately investigated, externally they appear identical. The petiole is only distinguished from the rachis as the portion of the leaf axis between the pulvinus and the first pair of pinnae. In regard to the development, Kaplan (1980) found late intercalary divisions produced the petiole; however the same could be said of the rachis. If the same process produces both the petiole and the rachis, then it is a mistake to attempt to subdivide the leaf axis into these separate structures. Identifying the full combination of processes that underpin the development of a 'phyllode' from initiation to maturity, and determining how these differ from the processes in other leaves may bring further insight.

Historically, morphological investigation has relied on establishing homology of classical components. In the case of the phyllode these have been the petiole, rachis, lamina and various meristems. Modern developmental genetics is identifying genes and gene families that operate in different domains, allowing a new conceptual framework for leaf morphology. Gene families such as YABBYs and Class III HD-ZIPs have been identified (see Bowman *et al.* 2002) that are responsible for establishing adaxial and abaxial cell identity, and consequently lamina outgrowth. Class I KNOTTED-like homeobox (KNOX) genes are expressed throughout the shoot apical meristem and play a role in the maintenance of meristem identity and cell indeterminacy, but have also been identified as playing a role in leaf complexity (Bharathan *et al.* 2002). These observations are directly relevant to the processes responsible for creating and maintaining structures, avoiding the classical reliance on the transformation of one structure into another. Process homologies can be established by comparing the identities and expression patterns of key regulatory genes in species from different plant families, and comparisons made between their expression patterns. These techniques give us a new opportunity to reappraise *Acacia* phyllodes and bipinnate foliage by directly investigating the actual developmental process involved in their creation.

Conclusion

Three hypotheses of *Acacia* phyllode homology have been proposed since Candolle first used the term 'phyllodium' (Table 1). The petiole hypothesis arose primarily from observations of seedling transitions and has been called into question by later work on coppice reversion shoots that suggested the petiole-rachis homology; however both have remained in common usage. Boke proposed the hypothesis that the phyllode was equivalent to the entire bipinnate leaf but derived from a different meristem. Kaplan supported the lamina equivalence of the phyllode blade but disagreed with the developmental pathway proposed by Boke.

Through all these investigations the goal has been to identify the homology of the 'endpoint', the phyllode, when compared to other plant structures. The hypotheses of structural homology themselves have led to our understanding that the phyllode is functionally and positionally a leaf. The *Acacia* phyllode may not strictly be a 'phyllode', yet it is markedly different from a "normal" foliage leaf and this difference is worthy of study. Process morphology is revealing the details of plant growth and allowing comparisons between apparently disparate organs. It is not names and labels, but ultimately the progress of ideas, facilitated by new approaches and better models, that will help us comprehend the phyllode's strangeness and deepen our understanding of plant form.

Acknowledgments

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Three new *Acacia* species (Fabaceae: Mimosoideae) from East Gippsland, Victoria

a235993

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Introduction

During field studies in 1985 in the eastern sector of the Benambra–Limestone Road, East Gippsland, we observed three *Acacia* taxa of dwarfed stature occurring sympatrically amongst a number of other free-flowering and free-seeding *Acacia* species. One of these taxa (here described as *Acacia infecunda*) appeared to have affinities with *A. boormanii* and a second taxon (here described as *A. nanopravissima*) showed affinity with *A. pravissima*. The affinities of the third taxon (here described as *Acacia tabula*) did not appear to be with any known taxon although a superficial similarity has suggested a relationship with *Acacia buxifolia* (Maslin 1996c, 2001c, Ross & Walsh 2003, Walsh & Stajsic 2007).

Subsequent morphometric and flavonoid analyses (Molyneux and Whiffin unpub. data) suggested that *A. tabula* is likely to be a stabilised hybrid between ancestral forms of *A. infecunda* and *A. nanopravissima*. While both *A. infecunda* and *A. tabula* are only known from the type locality, *A. nanopravissima* is known from a second small population at a site 3.5 km to the east of the type locality. Here it is represented by five ramets.

On specimens lodged earlier at MEL, we recorded much smaller population sizes for two of these taxa than subsequent investigation demonstrated. Prior to the January 2003 wildfires, the three new species were represented by approximately 50 mature 'plants' (ramets or stems) of *A. infecunda*, approximately 130 mature 'plants' of *A. nanopravissima* (MEL 1587015 noted approximately 40 plants) and approximately 140 mature 'plants' of *A. tabula* (MEL 1587014 noted 200 plants).

In February 2004, Carter (2004) only recorded approximately 50 reshooting ramets of *A. nanopravissima* and no regeneration of either *A. infecunda* or *A. tabula*. In February 2005 we recorded about 75 ramets of *A. nanopravissima*, 8 ramets of *A. infecunda* and 30 ramets of *A. tabula*, indicating that two years after the fires, regeneration, although initially slow, had occurred for all three species.

In over twenty-two years of field observations and growing trials, we have not observed any seed set on any of the three taxa, nor have we observed any incipient pods. Unpublished electroscan microscopy (SEM) undertaken at Monash University in July 1993 by Gunta Jaudzems clearly shows four pollen grains escaping an anther of *A. nanopravissima*.

Abstract

Three new species of *Acacia* with restricted known distribution in the Alpine National Park, East Gippsland, *Acacia infecunda*, *Acacia nanopravissima* and *Acacia tabula*, are described and illustrated. The postulated origin of *A. tabula* is discussed, utilising both morphometric and flavonoid information (Molyneux and Whiffin unpub. data) and the relationship between *A. infecunda* and *Acacia boormanii* is discussed, as is the relationship between *A. nanopravissima* and *Acacia pravissima*. The three new species are free-flowering but apparently infecund and appear to spread vegetatively by ramet formation from root suckers.

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(Micrograph 4, 35 mm transparencies of these images are available on request). Jaudzems, in a report of 26 July 1993 to one of us (WMM), stated that she had carried out viability tests on 47 grains of pollen collected from the anthers of *A. nanopravissima* and tested their viability using the method of O'Brien and McCully (1981). Jaudzems stated that tests showed that 68% of the pollen was viable, 21% questionably viable, and 11% was non-viable. Jaudzems also stated that this level of viability was low when compared with related species, but suggested that non-viability would not appear to be the reason for infecundity in *A. nanopravissima*. In another set of SEM scans, five rows of distinctly collapsed ovules are evident in a specimen of *A. tabula*. We offer no explanation for the lack of seed production but suggest it may be due to an as yet unrecognised post-zygotic event.

Taxonomy

1. Acacia infecunda Molyneux & Forrester *sp. nov.*

Ab A. boormanii Maiden habitu minore obligato repullulanti a radicibus, sterilibus, capitulis et phyllodiis minoribus differt.

Type: VICTORIA: near Benambra-Limestone Road, 14.viii.1995, W.M. Molyneux and S.G. Forrester. *s.n.* MEL 2312468 (holo: MEL; iso: AD, BRI, HO, NSW, PERTH).

A small erect shrub 30–60 (–120) cm high, 40–60 cm wide, extending asexually by the production of ramets; branchlets glabrous. Phyllodes linear, 12–41 mm long, 0.8–2.2 mm wide, straight, obliquely and excentrically mucronate, thin, grey-green, glabrous; mid nerve evident or obscure, anastomosing nerves absent, adaxial and abaxial width equal; gland small, not prominent, 4.8 (–11.5) mm above pulvinus. Inflorescence racemose; flower heads globular, axillary, one per axil; raceme axis (3–) 10–30 (–40) mm long; racemes of (5–) 8–10 heads. Peduncles 1.5–4 mm long. Flowers five-merous, 3–5 mm diameter, 5–9 flowers per head, golden, infecund.

Representative specimen examined: **VICTORIA:** Splitters Creek crossing, Limestone Creek Raad. Natmap 8524 Jacobs River 1:100,000 FV055095, 30.iv.1986, Molyneux & Forrester *s.n.*

Distribution: Acacia infecunda is apparently endemic to the Wulgulmerang district in East Gippsland, Victoria, where it is currently known by a single small population on the Wombargo Range in the upper catchment of Little River, a tributary of the Snowy River. The population comprises small fragmented stands in close proximity

Figure 1. Marphology of the three new *Acacia* species. Fram left to right: *Acacia infecunda, A. tabula and A. nanapravissima.*

extending along an approximate north-east to south-west line on a rocky slope near Benambra-Limestone Road.

Conservation Status: Using the criteria of the IUCN (2001), the species would be assessed as critically endangered, with a conservation code of CR D, on account of its exceedingly small population size, which may comprise no more than a single genetic individual or genet, which renders the species highly susceptible to fire or other stochastic events.

Habitat: The three new taxa share a dry woodland and heathland habitat on rocky slopes with soils derived from Devonian acid rhyolites. Associated understorey species include members of the Ericaceae, Dilleniaceae, Myrtaceae and Poaceae with an overstorey dominated by *Eucalyptus pauciflora, E. rubida* and *E.* sp. aff. *dives. Acacia amoena, A. gunnii* and *A. kybeanensis,* all of which are fecund, are also found growing in close proximity to the three new taxa.

Phenology: Flowers late August to early October.

Notes: Maslin (1996a, 2001a) notes that a "slow-growing dwarf variant" of *A. boormanii* occurs on high rocky ground at Splitters Creek, in the upper catchment of Little River, between Suggan Buggan and Wulgulmerang. Maslin (2001d) lists the species as *Acacia infecunda* Molyneux (ms). The new species is listed as *Acacia* sp. aff. *boormanii* (Wulgulmerang) in the seventh and eighth editions of A Census of the Vascular Plants of Victoria (Ross & Walsh 2003, Walsh & Stajsic 2007).

Etymology: The specific epithet refers to the apparent infecund nature of the species compared to the closely related *A. boormanii.*

Recommended English name: **Famine Wattle**

2. *Acacia nanopravissima* Molyneux & Forrester *sp. nov.*

Ab A. pravissima phyllodiis et inflorescentibus minoribus, plerumque habitu minoribus e fructibus non evolutis differt.

Type: VICTORIA: near Benambra-Limestone Road, 27.viii.1993, W.M. Molyneux and S.G. Forrester *s.n.* (holo: MEL 2312470; iso: AD, BRI, NSW, PERTH).

A small erect shrub 40–60 (–100) cm high, 25–40 cm wide, extending asexually by the production of ramets; branchlets glabrous. Phyllodes 3–8 mm long, 4–8 mm wide, strongly inequilateral, generally obdeltate, with the adaxial margin conspicuously rounded, grey-green, glabrous, imperfectly two-nerved, anastomosing nerves absent, adaxial width greater than abaxial width; gland prominent, (1.6–) 2.3–3.7 (–4.5) mm above pulvinus. Inflorescence, racemose, flower heads globular, axillary, one per axil; raceme axis (5–) 12–27 (–60) mm long, racemes of (8–) 6–10 heads. Peduncles 2–4 mm long. Flowers five-merous, 3–4 mm diameter, 7–9 flowers per head, golden, infecund.

Representative specimens examined: **VICTORIA:** Splitters Creek, Wulgulmerang, 11.i,1949, N.A.Wakefield *s.n.*: MEL 544638 (as *Acacia pravissima*); Little River, Black Mountain, 13.i.1949, N.A.Wakefield *s.n.* (as *Acacia pravissima*); Little River at Rockbank, Wulgulmerang, 'very localised', 29.xi.1962, J.H. Willis *s.n.*: MEL 1500988 (as *Acacia pravissima*); Wulgulmerang, Little River, 15.i.1971, A.C. Beauglehole: MEL 563409; Cultivated at Dixons Creek, 30.iv.1986, Molyneux & Forrester *s.n.*: MEL 252761; Splitters Creek crossing, Limestone Creek Road, c. 5.5 km west of Wulgulmerang-Suggan Buggan Road, 30.iv.1986, Molyneux & Forrester *s.n.*: MEL 1545132; Splitters Creek crossing, Limestone Creek Road, 22.ix.1990, Molyneux & Forrester *s.n.*: MEL 1587015.

Distribution: Acacia nanopravissima is apparently endemic to the Wulgulmerang district in East Gippsland, Victoria, where it is currently known by a single small population on the Wombargo Range in the upper catchment of Little River, a tributary of the Snowy River. The population comprises small fragmented stands in close proximity extending across a slope overlooking and south of Splitters Creek, a tributary of Little River, near Benambra-Limestone Road, with one small isolated stand of five plants on either side of Little River, east of the Splitters Creek subpopulation and east of the Benambra-Limestone Road.

Conservation Status: Using the criteria of the IUCN (2001), the species would be assessed as critically endangered, with a conservation code of CR D, on account of its exceedingly small population size, which may comprise no more than two genetic individuals or genets, which renders the species highly susceptible to fire or other stochastic events.

Habitat: The species occurs in dry woodland and heathland habitat on rocky slopes with soils derived from Devonian acid rhyolites. Associated understorey species include members of the Ericaceae, Dilleniaceae, Myrtaceae and Poaceae with an overstorey dominated by *Eucalyptus pauciflora, E. rubida* and *E.* sp. aff. *dives. Acacia amoena, A. gunnii* and *A. kybeanensis,* all of which

Table 1. Comparison of morphological characters for five species of *Acacia*: *Acacia infecunda, Acacia boormanii, Acacia nanopravissima, Acacia pravissima* and *Acacia tabula.*

Character	*A. infecunda*	*A. baarmanii*	*A. nanopravissima*	*A. pravissima*	*A. tabula*
Habit					
Size	Small, root-suckering shrub	Small to large shrub	Small root-suckering shrub	Medium to large shrub	Small root-suckering shrub
Shape	Erect	Erect to spreading	Erect	Spreading	Erect
Height	0.3–0.6 (-1.20) m	0.5–5 m	0.4-0.6 (-1) m	(0.5-) 3–8 m	0.25–0.50 m
Width	0.4–0.6 m	1–5 m	0.25–0.4 m	(1-) 4–8 m	0.20–0.45 m
Phyllodes					
Shape	Linear, excentrically mucronate	Linear or occasionally subterete, excentrically mucronate	Strongly inequilateral, generally obdeltate, adaxial margin conspicuously rounded	Strongly inequilateral generally obdeltate, adaxial margin conspicuously rounded	Inequilaterally narrowly oblong, elliptical, excentrically mucronate
Nerve	Single, adaxial and abaxial width equal	Single, adaxial and abaxial width equal	Imperfectly two-nerved, adaxial width greater than abaxial	Imperfectly two-nerved, adaxial width greater than abaxial	Single, adaxial width mostly greater than abaxial, occasionally equal
Gland	Single 4–8 (-11.5) mm above pulvinus	Single 2.5–10 (-19) mm above pulvinus	Single 1.6–3.7 (-4.5) mm above pulvinus	Single 1.5–5.5 (-9.5) mm above pulvinus	Single 1.5–4.4 (-6.5) mm above pulvinus
Length	12–41 mm	25–90 mm	3–8 mm	6–20 mm	6–17 mm
Width	0.8–2.2 mm	0.5–3 mm	4–8 mm	4–20 mm	0.8–2.5 (-4.2) mm
Inflorescences					
Arrangement	racemose	racemose	racemose	racemose	racemose
Axis length	(3-) 10–30 (-40) mm	30–60 mm	(5-) 12–27 (-60) mm	50–100 mm	(5-) 8–10 (-12) mm
Heads per raceme	(5-) 8–10	5–10	6–10	10–12	5–10
Peduncle length	1.5–4 mm	3–4 mm	2–4 mm	4–6 mm	1.5–3 mm
Flowerheads					
Flowerhead shape	globular	globular	globular	globular	globular
Diameter	3–5 mm	6–8 mm	3–4 mm	5–6 mm	3–5 mm
Flower number per head	5–9	5–10	7–9	8–12	5-8
Seed					
	Unknown	Yes	Unknown	Yes	Unknown
Suckering					
	Obligate	Occasionally	Obligate	Not known for sucker	Obligate

are fecund, are also found growing in close proximity to the species. The small outlying stand on Little River is associated with *Bursaria spinosa* and *Lepidosperma laterale* below an overstorey dominated by *E. camphora*.

Phenology: Flowers late August to early October.

Notes: Maslin (1996b, 2001b) notes that a "dwarf variant" of *A. pravissima* occurs at Splitters Creek, in the upper catchment of Little River, between Suggan Buggan and Wulgulmerang. Maslin (2001d) lists the species as *Acacia nanopravissima* Molyneux (ms). The new species is listed as *Acacia* sp. aff. *pravissima* (Wulgulmerang) in the seventh and eighth editions of A Census of the Vascular Plants of Victoria (Ross & Walsh 2003, Walsh & Stajsic 2007).

Etymology: The specific epithet refers to the species being smaller in all its parts to the closely related *A. pravissima*.

Recommended English name: **Little Kooka Wattle**

3. *Acacia tabula* Molyneux & Forrester *sp. nov.*

Ab A. infecunda *Molyneux & Forrester phyllodiis brevioribus latioribus asymmetricis differt; ab A. nanopravissima Molyneux & Forrester phyllodiis anguste oblingis differt.*

Type: VICTORIA: near Benambra-Limestone Creek Road, 22.x.1990, W.M. Molyneux and S.G. Forrester *s.n.* MEL 2312472 (holo: MEL; iso: AD, HO, NSW, PERTH).

A small erect shrub 25–50 cm high, 20–45 cm wide; extending asexually by the production of ramets; branchlets glabrous. Phyllodes 6–17 mm long, 0.8–2.5 (–4.2) mm wide, inequilateral, narrowly oblong, elliptical, excentrically mucronate, grey-green, glabrous; mid-nerve evident, adaxial width mostly wider than abaxial, seldom of equal width; gland evident, 1.5–4.5 (–6.5) mm above pulvinus. Inflorescence racemose; flower heads globular, axillary, one per axil; raceme axis (5–) 8–10 (–12) mm long, racemes of (5–) 8–10 heads. Peduncles 1.5–3 mm long. Flowers five-merous, 3–4 mm diameter, 5–8 flowers per head, yellow, infecund.

Representative specimens examined: **VICTORIA:** Splitters Creek, 9.ix.1962, Keith C. Rogers, *s.n.*: MEL 600258 (as *Acacia buxifalia*); Splitters Creek 2, 3.xii.1962, J.H. Willis *s.n.*: MEL 1500159 (as *Acacia* sp.); 'dry hills in *Eucalyptus maculasa* [*E. mannifera*], *E. dives* forest associated with *Acacia pravissima*' [*A. nanopravissima*], 3.xii.1962, J.H. Willis *s.n.*: MEL 1500159 (as *Acacia buxifalia*); Splitters Creek above Limestone Creek Road, 30.iv.1986, Molyneux & Forrester *s.n.*: MEL 1545133; Splitters Creek *c.* 10 km south-west of Suggan Buggan, 9.ix.1962, K.C. Rogers *s.n.*: MEL 600258; Map Ref: 8524 Jacobs River FV092053, 22.ix.1990, Molyneux & Forrester *s.n.*: MEL 1587014.

Distribution: Acacia tabula is apparently endemic to the Wulgulmerang district in East Gippsland, Victoria, where it is currently known by a single small population on the Wombargo Range in the upper catchment of Little River, a tributary of the Snowy River. The population comprises small fragmented stands in close proximity extending across a slope overlooking and south of Splitters Creek, near Benambra-Limestone Road.

Conservation Status: Using the criteria of the IUCN (2001), the species would be assessed as critically endangered, with a conservation code of CR D, on account of its exceedingly small population size, which may comprise no more than a single genetic individual or genet, which renders the species highly susceptible to fire or other stochastic events.

Habitat: The species occurs in dry woodland and heathland habitat on rocky slopes with soils derived from Devonian acid rhyolites. Associated understorey species include members of the Ericaceae, Dilleniaceae, Myrtaceae and Poaceae with an overstorey dominated by *Eucalyptus. pauciflora, E. rubida* and *E.* sp. aff. *dives*. *Acacia amoena, A. gunnii* and *A. kybeanensis,* all of which are fecund, are also found growing in close proximity to the species.

Phenology: Flowers late August to early October.

Notes: Maslin (1996c, 2001c) notes that a "dwarf variant" of *A. buxifolia* subsp. *buxifolia* occurs at Splitters Creek, in the upper catchment of Little River, between Suggan Buggan and Wulgulmerang. Maslin (2001d) lists the species as *Acacia tabula* Molyneux (ms). The new species is listed as *Acacia* sp. aff. *buxifolia* (Wulgulmerang) in the seventh and eighth editions of A Census of the Vascular Plants of Victoria (Ross & Walsh 2003, Walsh & Stajsic 2007).

Etymology: The specific epithet derives from the Latin *tabula*, a plank or board. The nearby Splitters Creek was so named for the activities of timber workers who cut and split planks for farm buildings in the district.

Recommended English name: **Wombargo Wattle**

Discussion

While *Acacia infecunda* has an apparent affinity with *A. boormanii,* and *A. nanopravissima* an affinity with *A.*

pravissima, they are genetically isolated from these species by geographic location, and appear to have been so over a long period. The nearest stands of *A. boormanii* are on the Snowy River some 20 km to the east and at a much lower elevation. The nearest stands of *A. pravissima* are on the upper Gibbo River on the Benambra-Corryong Road some 90 km to the north-west of the type locality for the three new taxa. While such separation of populations is not uncommon for *A. boormanii* or *A. pravissima*, the dwarfed nature, infecund state and limited population size and range suggest an isolating event which has caused local populations of *A. infecunda* and *A. nanopravissima* to have evolved such states in a limited area and perhaps under a severe climatic regime. Such isolation may have been associated with a glacial event on the Kosciuszko Plateau in the Late Quaternary. Hills (1975) states that periglacial conditions would have existed in the form of permafrost at that time around the Cobberas and Mt Wombargo. It was to this event that he attributes the development of the extensive 'rock rivers' in both these regions. Mount Wombargo is situated only 4 km to the north-west of the Type locality for the three new taxa and it would seem reasonable to postulate that *Acacia* populations in the region could have adapted to and survived these prolonged geological events by dramatic morphological reduction in stature and organ size and reproductive strategy.

The sympatric occurrence of the new taxa with free-seeding *Acacia* species such as *A. amoena*, *A. gunnii* and *A. kybeanensis* (pers. obs.) suggest recent migration by these species to the area from sites at lower elevations as the climate warmed during the Holocene. McKenzie (1997), who constructed pollen profiles from the late Quaternary for Victorian sites above 900 m elevation, demonstrates that much of the herbaceous alpine flora disappeared at ± 13,500 BP, to be replaced by upwardly migrating *Acacia*, *Eucalyptus*, *Nothofagus* and *Pomaderris* species as the climate became warmer. *Acacia infecunda*, *A. nanopravissima* and *A. tabula* may not be the only taxa to have been modified by localised past events. On a slope above Native Dog Flat, in the Upper Buchan River catchment, we have recorded a population of *Hakea* with affinities to *Hakea lissosperma*. This entity, which covers an area of approximately 0.2 ha, is dwarfed in habit (mostly under 1 m), extends by ramets and, whilst free-flowering, is also infecund.

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Some case studies of *Acacia* as weeds and implications for herbaria

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Introduction

There are a number of striking examples of Australian *Acacia* spp. occurring as weeds in other countries (New 1984). For example, Roux (1961) documents the introduction of *Acacia cyanophylla* Lindl. (now synonymous with *A. saligna* (Labill.) H.L.Wendl.) and *A. cyclops* A.Cunn. ex G.Don to the Cape Flats of South Africa for soil stabilisation in c. 1845 and their subsequent establishment and spread to the exclusion of other forms of vegetation by the 1890s. Both species are major environmental weeds in South Africa (Orchard & Wilson 2001b), although the impact of *A. saligna* has been reduced in that country following release of a genotype of the gall-forming rust *Uromycladium tepperianum* (Sacc.) McAlpine (Wood & Morris 2007).

There are 1381 described species of *Acacia sens. lat.* worldwide, 993 of these occur in Australia, most of which are now in the genus *Acacia sens. str.* (formerly *Acacia* subgen. *Phyllodineae*, synonym *Racosperma*) (Maslin 2004). Current data shows that 24 taxa of Australian acacias are naturalised in Victoria, ten of these are Victorian taxa naturalised outside their indigenous range, and a further three Australian species are incipiently naturalised in Victoria (Walsh & Stajsic 2007).

In this paper we compare four generally similar *Acacia* species occurring on the Victorian coast between Queenscliff and Torquay (an estimated total coast length of 28 km). One is an indigenous species in the study area, occurring in scattered remnant populations. The other three are introduced species from other parts of Australia that have become naturalised in the study area. These naturalised species have presented a number of problems in relation to their identification, status (indigenous or introduced) and management.

From late 2000 to 2002, staff at the National Herbarium of Victoria (MEL) received *Acacia* specimens, sent for identification from Barwon Heads and Torquay by collectors believing that they may be unusual forms of indigenous *Acacia uncifolia* (J.M. Black) O'Leary (previously *Acacia retinodes* Schltdl. var. *uncifolia* J.M.Black). During this process we became aware that two different species of *Acacia* were being mistaken for *A. uncifolia*, and at least one was being used in revegetation projects in the study area. Both species were known weeds in other places. In late

Abstract

A context for Australian *Acocia* species (wattles) as weeds is provided, both overseas and within Australia. Specific case studies from the western Victorian coast between Queenscliff and Torquay are used to illustrate some of the problems and challenges provided by weedy acacias, including confusion between indigenous and introduced species. Four species, one indigenous (*Acocio uncifolia*) and three introduced (*A. cupularis*, *A. cyclops* and *A. rostellifero*), are described and the reasons for their occurrence in the study area are investigated. Some key factors for the success of acacias as weeds are outlined. Possible implications for the future role of herbaria in assisting land managers to resolve weed issues are discussed and predictions about the changing role of herbaria in relation to weed issues are made.

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2004, a third similar *Acacia* was collected in the same area and sent to MEL for identification. Based on the South African experience noted above at least one of these species, *Acacia cyclops*, has the potential to create a 'weedy wattle' monoculture along the coast between Queenscliff and Torquay.

This paper does not aim to survey all acacias naturalised in the study area, but to focus on three introduced species that are superficially similar to *A. uncifolia* and to highlight issues common to many weed invasions. The presence of newly recorded weed species and their distinction from indigenous plants in the Victorian flora provides increasing challenges for botanists and land managers. This study documents in detail the steps and processes involved in the identification and assessment of three newly recognised naturalised acacias, and in doing so provides a general methodology for resolving some of the questions commonly arising from weed invasions. This methodology will be most suitable for application by botanists with access to herbarium-based resources and may form the basis for an increasing involvement in the resolution of weed issues by herbaria in the future.

Some authors use the terms 'indigenous' and 'native' as synonyms (Pyšek *et al.* 2004; Bean 2007). We consider it useful, at least in relation to this study, to distinguish between them. For the purposes of this paper, indigenous is defined as 'occurring naturally in a particular locality' and native is 'occurring naturally (indigenous) somewhere in Australia'. We acknowledge that these definitions may not adequately cover the concept of local provenance or genetic stock.

Methods

Fresh and dried plant material of *Acacia* species requiring determination was received by the National Herbarium of Victoria. The identifications of *Acacia cyclops*, *A. rostellifera* Benth. and *A. cupularis* Domin in the study area were completed using botanical literature, herbarium specimens and examination by *Acacia* specialists. A field trip was undertaken to the coastal area between Queenscliff and Torquay to collect voucher specimens of *Acacia uncifolia* and the weed species, and to assess the extent of the invasion of the weed species. The status (indigenous or introduced) of all acacias in this study was determined using herbarium specimens, distribution information and advice from *Acacia* specialists. An assessment of the means and timing of the introductions of the three naturalised acacias was made using various historical documents and communications with *Acacia* experts and people with relevant knowledge of the study area. Specimens of the three naturalised acacias were compared with all other specimens of these taxa held at MEL as part of our efforts to predict source localities and means of introduction. Morphological descriptions and distribution information was collated from relevant texts, specimens from the study area and other MEL specimens, and a table of key characters for differentiating the four species was created.

Results

Status – introduced or indigenous?

Acacia cyclops and *A. rostellifera* are not indigenous anywhere in Victoria, therefore the decision that they are introduced to the study area was straightforward. However, because indigenous populations of *A. cupularis* occur in western Victoria, some consideration was given to this species being indigenous in the study area. Except for a collection by A. C. Beauglehole of *A. cupularis* from Deep Creek, Torquay within the study area in 1983, no coastal populations of this species are known east of the South Australian border. Given that there are no coastal collections of *A. cupularis* in Victoria before 1983 the authors, in consultation with B. Maslin (Western Australian Herbarium) and M. O'Leary (State Herbarium of South Australia), decided that the plants at Deep Creek are most likely introduced. Except for nine seedlings observed at Ocean Grove following a fire in 2001, only a few well established individuals of *A. cupularis* have been observed by us in other parts of the study area, all occurring in highly modified sites. In addition, a number of old plants of *A. cupularis* were reported from bushland at Barwon Heads (B. Wood pers. comm.). We consider that all of these plants are most likely introduced, and at least some by deliberate planting.

The general morphology (mainly phyllode shape and size) of *A. cupularis* collections made by the authors from Queenscliff, Torquay and Ocean Grove in 2004 (MEL 2278496, MEL 2278498, MEL 2278499),

was compared with all collections of this species from Western Australia, South Australia and Victoria held at MEL. No matches were obtained with specimens from Western Australia. The best matches, based on general morphology are with some specimens from South Australia and Victoria. Essential details of these collections are presented in Table 1. It should be noted that there are additional South Australian and Victorian *A. cupularis* collections in MEL that do not match the Queenscliff and Torquay collections. A young post-fire regenerated plant (MEL 2278497) from Ocean Grove has been excluded from morphological comparison because it has longer and broader phyllodes, which are likely to be juvenile characteristics. Based on our morphological observations, the source locality or localities of the Queenscliff and Torquay populations of *A. cupularis* are more likely to be in South Australia and/or Victoria.

Species descriptions

Acacia uncifolia (indigenous)

Acacia uncifolia is a bushy shrub or tree 5–10 m high. This species has narrow one nerved phyllodes, 30–65 mm long by 3–10 mm wide, with a hooked (uncinate) tip and mucro (Orchard & Wilson 2001a). Inflorescences are short racemes, usually with 3–10 pale yellow globular heads. Pods are linear, with slight constrictions between seeds, and are somewhat papery or leathery. Seeds are ¾ or more encircled by a red-brown to blackish funicle and have a creamy yellow aril at one end.

Acacia cupularis (introduced)

Acacia cupularis is usually a shrub 1–2.5 m high. This species has narrow phyllodes with a single nerve. The phyllodes are generally linear, straight and 30–70 mm long by 1–4 mm wide (Orchard & Wilson 2001a). As currently circumscribed, this species shows considerable variation in phyllode morphology. In the study area phyllodes are mostly 30–50 mm long by 3.5–6.0 mm wide, with a straight tip and mucro. Inflorescences are short racemes with only 2 or 3 globular golden heads in each. Pods are constricted between seeds and break readily at the constrictions. The seed is described by Orchard and Wilson (2001a) as having a small orange to red funicle/aril at one end of the seed, however in specimens from the study area the funicle/aril is brown.

Acacia cyclops (introduced)

Acacia cyclops is a shrub or small tree 1–6 m high. This species has narrow phyllodes with 3–4 distant main nerves. The phyllodes are 40–95 mm long by 6–15 mm wide (Orchard & Wilson 2001b). In the study area phyllodes are mostly 40–80 mm long by 5–11 mm wide, with a more or less straight tip. Inflorescences are short racemes with 1 or 2 globular golden heads. Pods are linear, not constricted between the seeds and quite

Table 1. MEL specimens of *Acacia cupularis* that are most morphologically similar to *A. cupularis* specimens from the study area.

MEL number	Locality	Collector	Date collected
Victoria			
1500511	Lochiel near Dimboola	Lowe, J.H.	24 October 1920
1500514	Dimboola	Lowe, J.H.	October 1920
523611	Victoria	Unknown	Unknown
2040703	Torquay-Barwon Heads Coastal Reserve	Beauglehole, A.C.	17 January 1983
South Australia			
2073884	?Mooroogoopa, possibly in the vicinity of Guichen Bay	?Schulzen, L.W.	July 1850
627607	c. 12km from Mount Hope toward Elliston, beside Lake Hamilton	Canning, E.M.	2 December 1982
2073876	Near Port Augusta	Giles, E.	1880
2073880	Yorke Peninsula	Tepper, J.G.O.	1879

thick and leathery. Seeds have a bright orange to red funicle/aril that completely encircles the seed.

Acacia rostellifera (introduced)

Acacia rostellifera is a dense shrub or small tree to 6 m high. This species has narrow phyllodes, with one or sometimes two nerves, 45–115 mm long by 3–17 mm wide (Orchard & Wilson 2001a). In the study area phyllodes are mostly 65–110 mm long by 5–10 mm wide, with a hooked (uncinate) tip and mucro. Infloresences are short racemes with 3–9 golden globular heads. Pods are constricted between the seeds and break readily at the constrictions. Seeds have a large orange funicle/aril at one end of the seed.

Distributions, history in the study area and means of introduction and subsequent spread

For all species the Australian distribution is given, and for the introduced species, a discussion of their discovery in the study area, notes on possible means of introduction and subsequent spread are provided.

Acacia uncifolia (indigenous)

This species is indigenous along the coast in Victoria in three main centres of distribution: Wilsons Promontory, the southern part of the Mornington Peninsula and the Bellarine Peninsula near Geelong to as far west as Point Impossible near Torquay. It is also found in coastal areas of South Australia on Kangaroo Island and the Fleurieu Peninsula, and on King and Flinders Islands in Bass Strait.

Acacia cupularis (introduced)

Acacia cupularis is indigenous in coastal and near coastal areas from Albany WA through South Australia to the Victorian border. Small populations also occur a considerable distance from the coast throughout its range including in western Victoria. A small naturalised population (of a different phyllode variant to the one in the study area) is known from Royal Park (MEL 2012013, MEL 2144434) in the Melbourne suburb of Parkville.

Sterile material of *A. cupularis* was collected at Deep Creek, Torquay by G. Stockton and sent to MEL in 1996 but remained undetermined until a flowering and fruiting specimen was collected by Stockton from the same locality in October 2000 (MEL 2156628). This collection was brought to MEL for confirmation of identification, prior to propagation for revegetation works. Stockton noted that the plants at Deep Creek were different from plants of *A. uncifolia* with which he was familiar. After thorough examination of *A. retinodes* specimens held at MEL a match for this specimen (Beauglehole MEL 2040703) was found in the herbarium incorporated as *A. uncifolia*. The Beauglehole specimen was collected in 1983 in the same area as the Stockton collection. However, it was noted that these two collections did not resemble other *A. uncifolia* specimens held at MEL and that the Beauglehole specimen was incorrectly determined. Subsequent examination in March 2003 by D. Murphy (MEL) and M. O'Leary (State Herbarium of South Australia) identified these specimens as *A. cupularis*.

In 2004, an additional population of *A. cupularis* was recorded from dune vegetation in the Buckley Park Foreshore Reserve on the south side of Collendina Caravan Park at Ocean Grove. In this area a fire in February 2001 had stimulated seedling germination of *A. cyclops, A. saligna* and nine individuals of *A. cupularis* (B. Wood pers. comm.). Large well established plants of *A. cupularis* are also present in Barwon Heads Caravan Park and on roadsides in Ocean Grove (B. Wood pers. comm.) and near Queenscliff, leading to speculation that this species was deliberately introduced for horticulture some years ago. It is not known if plants from the initial introductions of *A. cupularis* have been used as a seed source for indigenous revegetation in the mistaken belief that they were indigenous *A. uncifolia*.

Acacia cyclops (introduced)

This species is notably tolerant to saline soils and salt spray (Orchard & Wilson 2001b). It is indigenous in coastal and near coastal south-west Western Australia as far north as Leeman and east to the South Australian border. In South Australia it is found in disjunct localities on the coast as far east as the Yorke Peninsula. Populations on Kangaroo Island and east of Yorke Peninsula are probably introduced (Orchard and Wilson 2001b). At MEL there is a 1994 record (MEL 2021046) of a single plant in coastal dune vegetation at Narrawong, near Portland in western Victoria.

By the time it was first identified in the study area in 2002, *A. cyclops* had become well established at Barwon Heads, including on cliff-tops at The Bluff, where it occurs as a wind pruned shrub one to three metres high (Figure 1).

The 2001 fire in dune vegetation in Buckley Park Foreshore Reserve at Ocean Grove resulted in the germination of an estimated 1000+ seedlings of *A. cyclops*, presumably from soil-stored seed (B. Wood pers. comm.). In January 2002, M. Connell, a seed collector in the study area, contacted MEL regarding a suspected local form of *A. retinodes* with a conspicuous red funicle/aril encircling the seed. At this time he submitted to MEL three separate collections of this 'form' (MEL 2156625, MEL 2156626, MEL 2156627). These plants were determined by B. Maslin (Perth Herbarium) to be *A. cyclops*.

Deliberate planting for coastal dune stabilisation is a strong possibility for the initial introduction of *A. cyclops* to the area. *Acacia cyclops* has been used to stabilise coastal sand dunes overseas (Orchard & Wilson 2001b), most notably in Africa (where is has become a widespread weed), and it may have been recommended for a similar purpose by the Natural Resources Conservation League (NRCL) in Victoria (W. Chapman pers. comm.). However, *A. cyclops* does not appear on the list of species used for remedial works since 1967, to stabilise blowouts in the coastal dunes along the Barwon Heads to Torquay Road, including the area known as 13th Beach (Alsop 1984). It was listed in at least one nursery catalogue in the 1970s (Australflora 1978) and recorded as present in a survey of public gardens in Melbourne published in 1990 (Shann 1990). Before *A. cyclops* was identified as naturalised at Barwon Heads it had already been spread by deliberate plantings in the area under the assumption that it was *A. uncifolia*.

Acacia rostellifera (introduced)

This species is indigenous to coastal areas of south-west Western Australia, from Shark Bay in the north to Israelite Bay in the east.

Acacia rostellifera was listed in at least one nursery catalogue during the 1970s (Australflora 1978). In the 1960s and 1970s NRCL was growing and supplying a species listed as *A. cyanophylla* (Natural Resources Conservation League of Victoria c. 1970), Orange Wattle, now synonymous with *A. saligna*. At one time in its taxonomic history *A. rostellifera* was known as *A. cyanophylla* var. *dorrienii* Domin, leading us to speculate that the NRCL may have been supplying *A. rostellifera*. However, because the population of *A. rostellifera* recorded in this study is the first Victorian record, we consider that references to *A. cyanophylla* in the NRCL catalogues most likely refer to the more widespread *A. saligna*.

Acacia rostellifera was first noted as being naturalised in Victoria from two collections by B. Wood (MEL 2278502, MEL 2278503) at a section of 13th Beach known as 40W, made in October 2004. It had presumably been overlooked for many years despite occurring in an almost pure stand of over half a hectare (c. 90m x 70m, W. Chapman pers. comm.), near a major road. By this time the collector was familiar with the presence of weedy acacias in the Barwon Heads area and this population was suspected of being introduced. In Alsop's (1984) discussion of remedial works along the Barwon Heads to Torquay Road he described the planting in 1979 of 150 plants of *A. retinodes* (variety not specified) propagated from seed collected from a single tree growing on a sand dune in Torquay. We speculate that this planting may actually include at least some *A. rostellifera*. This is supported by the discovery of two fenced areas near the 40W carpark between Barwon Heads and Black Rock, one containing *A. uncifolia*, the other containing *A. rostellifera*, and both enclosing mature specimens housed within wire treeguards (B. Wood pers. comm.). It is not known if *A. rostellifera* has ever been collected and/or propagated from this site on the assumption that it was indigenous.

Discussion

Means and timing of introduction and spread of the three weedy species

Details of the introduction and subsequent spread of the three naturalised *Acacia* species in this study are probably impossible to confirm. Historical documentation of plantings is sparse and necessitates speculation of both means and timing of the initial introductions. The means of introduction has most likely been by deliberate planting for amenity or coastal sand-dune stabilisation. Nurseries specialising in Australian native plants for farms and gardens increased in prominence from about the late 1940s (Youl 1999) and as a result the range of native plants available to horticulture increased considerably from that time. The culture of enthusiastically bringing new native species into horticulture peaked in the 1960s

and early 1970s (Elliot 2002) and is possibly the context for deliberate introduction of the species under study here. Examination of nursery catalogues and plant lists supports the idea that many more *Acacia* species became available in the 1960s and 1970s. It seems likely that native plant enthusiasts helped to bring many of these plants into gardens and other plantings at this time. We consider that one possibility is that the three weedy species discussed in this paper were introduced to the Queenscliff to Torquay coast concurrently by a native plant enthusiast. At the same time (1960s and 1970s) Australian native (seldom indigenous) plants were being promoted and used for large scale land rehabilitation projects (Thompson 1968); of the three species under study here *Acacia cyclops* is the most likely to have been introduced in this way.

A significant secondary means of introduction is the deliberate propagation and spread of one, two or all of these *Acacia* spp. by people believing them to be part of the indigenous flora of the area. A contributing factor to this is misidentification, viz., the belief that one, two or all of these *Acacia* spp. was the indigenous *Acacia uncifolia*. The enthusiasm for including this species in indigenous revegetation projects was, and still is, largely driven by its relative rarity and its depletion since European settlement. The indigenous plant movement, which has grown since the 1980s, is the context for this approach. In addition, other means of local spread are possible including vegetative spread by root suckers (*A. rostellifera*), seed dispersal by ants and birds, and via movement of soil and plant material.

Various land uses and disturbance factors on the coast between Queenscliff and Torquay would have facilitated weed invasion as well as necessitating remedial works (Alsop 1984), which have also contributed to weed invasion. A specific example is the construction of the Barwon Heads–Torquay road (cut and progressively sealed from 1936, W. Chapman pers. comm.), resulting in the loss of indigenous vegetation and large blow-outs of sand by 1966 (Alsop 1984). Sluiter (1964) reports that plantings of introduced Marram grass (*Ammophila arenaria* (L.) Link) had already occurred in this area prior to 1964.

Figure 1. *Acacia cyclops* growing on the clifftops at The Bluff at Barwon Heads. The dark green shrubs closest to the sea are *A. cyclops*. Photograph D. Murphy.

Some traits of these acacias that predispose them to weediness

It is generally recognised that there are intrinsic biotic factors that predispose some acacias to weediness (McDonald *et al.* 2001). It is perhaps less recognised that certain cultural factors also contribute to weediness. Examples of both are discussed below.

Many *Acacia* species have the ability to reproduce clonally via the production of root suckers. Suckers may form as a result of root disturbance, including during control efforts to physically remove plants. *Acacia rostellifera* has been observed in the study area spreading vigorously via root suckers. One horizontal 'runner' measured 12 metres in length and had produced 18 shoots (B. Wood pers. comm.). *Acacia cyclops* is also known to sometimes produce suckers (Bartle *et al.* 2002) but has not been observed to do so in the study area. However, it does produce low lateral branches to five metres long at The Bluff at Barwon Heads (B. Wood pers. comm.) and has been observed to produce adventitious roots where lateral branches have contacted the ground (T. Wood pers. comm.).

All three species are hard-seeded, enabling long-term viability of seed in the soil seedbank. One established *Acacia* plant may be surrounded by enough soil-stored seed to constitute a major weed invasion when germination conditions occur. This enables a potential weed to progress from an apparently benign state to an environmentally harmful one in a very short time span, as well as adding complexity to attempted eradication programs.

All three species grow naturally in sand in coastal locations, predisposing them to successful colonization in the study area. *Acacia cyclops* is tolerant to sea spray and highly saline soils and it has become naturalised elsewhere in coastal environments (Orchard & Wilson 2001b).

Acacias are popular in horticulture because they possess a number of desirable features, such as prolific flowers, attractive foliage and rapid growth, among others. These features have attracted attention to the genus by nurseries and gardeners and combined with a lack of caution, have led to the wide dissemination of many Australian species. Some of these have become weeds.

Many *Acacia* species are superficially similar in growth form, and vegetative and floral features. Positive identification often requires some specialised knowledge of the genus and the examination of phyllodes, bipinnate leaves, flowers, pods and seeds. The three weed species examined in this paper are superficially similar to an indigenous species in the study area, *Acacia uncifolia*, especially when only vegetative material is available. The similarity of indigenous

Table 2. A comparison of key identification characters for the four acacias in the study area.

Character	*A. cupularis*	*A. cyclops*	*A. rostellifera*	*A. uncifolia*
Number of main nerves on phyllode	1	3–4	1	1
Phyllode length (mm)	30–50	40–80	65–110	30–65
Phyllode width (mm)	3.5–6.0	5–11	5–10	3–10
Flower colour	golden	golden	golden	pale yellow
Number of flower heads in inflorescence	2–3	1–2	3–9	3–10
Pod	constricted and readily breaking between seeds	not constricted and not readily breaking between seeds	constricted and readily breaking between seeds	slightly constricted and not readily breaking between seeds
Funicle/aril	small brown funicle/aril at one end of the seed	bright orange to red funicle/aril completely encircling seed	large orange funicle/aril at one end of the seed	red-brown to blackish funicle ¾ or more encircling seed and creamy yellow aril at one end

plants to weed species is not often recognised as a factor contributing to weediness but we believe it may become more important in the future. For the three weed species studied in this paper it is a major reason why they have been overlooked as weeds in the area and why one of these (*A. cyclops*) has been deliberately spread.

Implications for herbaria and future directions

This study documents some of the ways herbaria already support the resolution of weed issues and forecasts a likely greater role in future. Essentially this role, as exemplified by the current study, involves the provision of weed identifications and information to clients who are directly involved in weed management. Opportunities also exist for herbaria, using existing expertise and data, to contribute to the relevant parts of strategic programs concerned with weed issues.

Herbaria are likely to receive more "is it indigenous or is it introduced?" enquiries from land managers, probably at an increasing rate. The continuing fragmentation of remnant vegetation, the close proximity of introduced plantings to remnants, and the interest in indigenous revegetation (especially at the local level) are all likely to drive this trend. Such questions are, and will continue to be, challenging for herbaria to resolve. The occurrence of hybrids between indigenous and planted species (e.g. suspected *Grevillea rosmarinifolia* A.Cunn. hybrids near Melbourne), the existence of non-indigenous provenance plantings close to indigenous remnants and/or plantings of the same taxon, e.g., *Lomandra longifolia* Labill. in Greater Melbourne (Duxbury 2005), and gaps in the documentation of both remnant and planted vegetation, all add complexity to the factors already outlined in this paper. Some of these questions will probably not be resolvable.

As the central repository for botanical specimens and information in a particular geographic area, state herbaria have a clear responsibility to adequately document the flora (including the ever expanding weed flora) of that area. When new weeds are found it is important for them to be correctly identified and for collectors to lodge voucher specimens. This will require significant levels of interest and effort by collectors, many of whom only collect plant specimens

Figure 2. *Acacia rostellifera* regenerating from prolific root suckers after removal of mature plants at 13th Beach. Photograph B. Wood.

on an ad hoc basis, and a clear acknowledgment of the associated benefits by herbaria, management agencies and their funding bodies. Voucher specimens enable identifications to be verifiable over time and updated in line with taxonomic changes. Associated information on the specimen labels (e.g. distribution, habitat, abundance and impacts) provides added value. Adequate information about a particular weed enables assessment of its potential impacts, and hopefully leads to sufficient allocation of resources and management actions. It also allows state herbaria to disseminate this information to government agencies and the general public. An important part of this is the recognition of spotting characters (such as those listed in this study, Table 2) that enable land managers and other local workers to identify weed species and differentiate them from indigenous species in their area. Practical information such as this can form the basis for educational material and other publications.

Early detection of new weeds is desirable to enable a rapid response by managers. This has the potential to save considerable time, money and resources used for weed mitigation. For example, in the present study, *Acacia cyclops* is established to such an extent on the unstable cliff-top at The Bluff at Barwon Heads that removal is now complex and potentially costly. Given the absence of thorough, on-going statewide weed surveys, the discovery of new weeds relies largely on local vigilance and chance detection. Some of these chance detections are made by botanists in herbaria as part of their normal work, including identifications of unknown plant material submitted by clients, as in this study. State herbaria can make a significant contribution to plant conservation and biodiversity management by informing the relevant people and agencies about new weed discoveries. Opportunities also exist for some state herbaria to be involved in strategic plans to manage weed invasions. For example, The New Incursion Response Protocol in Tasmania (Boersma *et al.* 1999) and the Weed Alert Rapid Response Plan (WARR) in Victoria (Smith 2006) can only progress after formal confirmation of identity by the relevant state herbarium.

Molecular methods may be used to examine and identify the geographic origins of weeds in more detail in the future and may provide higher levels of resolution than morphological methods. Herbaria may be called upon to carry out these studies. Molecular identification methods are especially powerful when inadequate plant material limits morphological identification. As noted previously there are two critical questions faced by herbaria when confronted by an unknown plant: what is it and what is its status (indigenous or introduced)? For the identification of plant species there is hope that a database comprising DNA barcodes for all plants will be available in the future. However, there are some technical difficulties to be overcome before this is possible. DNA barcoding is still being developed for plants and application of this method will require herbaria to invest in appropriate staff and equipment.

The recent use of molecular data and advances in analysis techniques have already enabled the investigation of the origin and spread of invasive plant species (Schaal *et al.* 2003). The most common methods have used DNA fingerprinting or sequencing techniques and phylogeographic analysis (Schaal *et al.* 2003; O'Hanlon *et al.* 2000). In most cases these studies have focused on species in which the weed status of the plant is known prior to the study, and generally the invasive species is separated from its indigenous areas of distribution by a substantial geographic distance and/or barrier, such as the intercontinental occurrence of invasive species (e.g. Australian occurrences of *Acacia* (*Vachellia*) *nilotica* (L.) Del., a species indigenous to India and Africa, Wardill *et al.* 2005). However, it is uncertain how molecular studies would determine the origin and status of a plant species found a relatively short distance from known indigenous populations, such as *Acacia cupularis* in this study. Population genetic theory predicts that species with small and recent introductions will display low intra-population genetic diversity, due to founder effects and genetic bottlenecks; thereby providing a possible means of distinguishing weed populations from indigenous occurrences, when combined with other sources of evidence, e.g. historical herbarium records (Barrett 1996; Amsellen *et. al.* 2000).

It is likely that herbaria will continue to rely on the examination of morphological characters and historical data to resolve various weed questions in the short to medium term. We consider that molecular methods will complement rather than replace these traditional methods in herbaria.

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Biological control of Australian native plants, in Australia, with an emphasis on acacias

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Introduction

Australian native plants have been a source of fascination for horticulturists since their discovery by European explorers and settlers during the early colonisation of Australia (Elliot & Jones 1980; Cavanagh 1995, 2006). However, it was not until the 1950s, 180 years following Cook's maiden voyage, that Australian native plants surged in popularity with Australian gardeners, perhaps driven by recognition of their low-maintenance requirements, an increasing awareness and concern for the Australian flora, and a contribution to the search for national identity. At least 5,000 Australian native plants are recognised as horticulturally desirable (Elliot & Jones 1994), perhaps more if species used for revegetation and habitat restoration programs are included. *Acacia s.s.* (synonyms *Acacia* subgenus *Phyllodineae* and *Racosperma*, see Maslin 2008) Australia's largest plant genus (Maslin 2001) is a horticultural treasure trove with around 590 species recognised as suitable for cultivation (Elliot & Jones 1982), including taxa with a diverse array of ecological traits, canopy architecture, leaf shape, texture and colour, and floral features. Acacias were quickly taken into horticulture in Europe following colonisation of Australia, with *A. verticillata* (L'Her.) Willd. (Cavanagh 2006) being the first recorded species to flower in the northern hemisphere. A trans-global trade in Australian acacias soon followed, first inspired by horticultural interest, but largely driven later by agricultural-directed incentives including production of tannin, timber and pulp (Sherry 1971; Turnbull *et al.* 1998), fodder (Vercoe 1989; Thomson *et al.* 1994), food (Thomson 1992; Maslin *et al.* 1998), revegetation (Doran & Turnbull 1997) and erosion control (Shaughnessy 1980). Inevitably, Australian acacias are now naturalised in many locations including New Zealand, North and South America, Western Europe, Reunion Island, Britain and South Africa (Cadet 1981; Webb *et al.* 1988; Henderson 2001; USDA, NRCS 2006; Royal Botanic Gardens Edinburgh 2006) either as the result of intentional establishment programs, or as escapees from mostly well-intentioned horticultural activities. Many are now regarded as serious weeds where they threaten ecological, agricultural and water assets (Holm *et al.* 1979; van Wilgen *et al.* 2006). In Australia, broad-scale horticultural exploitation of acacias and other native plants has resulted in approximately 297 native vascular

Abstract

Australia's native flora is widely used in horticulture for amenity planting, windbreaks, garden ornamentals and revegetation programs. However, within Australia, native species utilised beyond their natural distribution have potential to naturalise and cause ecological harm in natural ecosystems with impacts similar to those caused by exotic plants introduced from overseas. In southern Australia, around 297 species of native plant are naturalised beyond their native range, including 41 species of *Acacia*. Loss of biodiversity through changes in biomass distribution, nutrient cycling, competition for resources, altered fire regimes and erosion patterns can be attributed to native plant invasions. Australian plants can be highly problematic overseas where many, particularly acacias, are subject to classical biological control. The principles of classical biological control can be applied to the suppression of weedy native plants in Australia, particularly priority trans-continental invaders, which include species of *Acacia, Billardiera, Hakea, Leptospermum, Melaleuca, Paraserianthes* and *Pittosporum*.

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plants naturalising in habitats beyond their natural range, including 41 species of acacias (Table 1, J Hosking, M. Baker, D. Cooke, G. Keighery pers. comm. 2006). While many are weak adventives or marginally naturalised, others impact on threatened flora and fauna (Coutts-Smith & Downey 2006), or may have impacts equivalent to problematic foreign invasive plants.

Impact of invasive acacias and other native plants

The ecological and economic impact caused by invasion of native plants in Australia is documented by few case studies, despite increasing awareness of the potential of native plants as weeds. The impacts of invasive native plants can include disruption to ecological processes by accelerated biomass accumulation, reduced light penetration, increased nitrification, changed fire intensity and frequency, altered geo-morphological processes, hybridisation with congeners, which can lead to declines in species richness and abundance (Carr *et. al.* 1992). Many of these impacts are similar to the invasion of plants originating from other countries (exotic plants). However, quantified impact data on biodiversity values are only published for *Pittosporum undulatum* Vent. (Mullett & Simmons 1995; Rose & Fairweather 1997; Mullett 1999), *Leptospermum laevigatum* (Sol. ex Gaertn.) F. Muell. (Molnar *et al.* 1989; Lam & van Etten 2002) and *Acacia longifolia* (Andrews) Willd. (McMahon *et al.* 1996; Costello *et al.* 2000).

The ecological impacts of invasive Australian plants, particularly acacias, are best studied in South Africa, where 13 *Acacia* species are naturalised, and eight species cause widespread transformation of biological communities and ecological processes (Henderson 2001; Richardson & van Wilgen 2004). While the same scale of invasion and impacts are yet to be realised from native acacias within Australia, circumstantial evidence indicates that the potential is there. Rapidly expanding populations of *A. longifolia*, *A. dealbata* Link, *A. pycnantha* Benth. and *A. decurrens* Willd. in Western Australia; *A. cyclops* Cunn. ex Don in South Australia; and *A. saligna* (Labill.) W.L. Wendl., *A. baileyana* F. Muell. and *A. longifolia* in eastern Australia indicate broad-scale

Table 1. Number of Australian native plant species naturalised outside their native range in Australian States and Territories

State	Local native species[1]	Interstate native species[2]	Invasive Australian acacias[3]	Invasive exotic acacias[4]	References
Western Australia	42	61	18 (17%)	3	J. Hosking pers. comm. 2006, G. Keighery pers comm. 2006;
South Australia	13	41	10 (18%)	2	www.flora.sa.gov.au, D. Cooke, J. Virtue, J. Hosking pers. comm. 2006
Victoria	49	59	25 (23%)	1	Carr (2001), Flora Information System 2006, J. Hosking pers. comm. 2006
Tasmania	8	19	5 29%)	0	Buchanan (2005), M. Baker pers. comm. 2006, J. Hosking pers. comm. 2006
New South Wales	60	17	13 (17%)	1	J. Hosking pers. comm. 2006
Queensland	6	13	3(16%)	2	J. Hosking pers. comm. 2006
Northern Territory	5	4	1 (11%)	1	J. Hosking pers. comm. 2006

[1]Australian taxa native to the State, but naturalised beyond their pre-European distribution.

[2]Australian taxa native to other States or Territories.

[3]Native Australian *Acacia* taxa (proportion (%) of the total number of Australian taxa naturalised for each State or Territory).

[4]Naturalised non-Australian *Acacia* taxa. Doubtful or unsubstantiated records or those species with questionable native status have been omitted, possibly underestimating the numbers of naturalised taxa.

impacts may be inevitable without the implementation of appropriate control measures. In Australia, 43 native acacias are naturalised beyond their native range, in addition to three species of exotic acacias (these exotic species are in the former *Acacia* subgenus *Acacia*, that will become *Vachellia*, see Maslin 2008) naturalised in eastern and Western Australia (Table 1). In nearly all cases, invasions can be attributed to horticultural trade and the subsequent spread of plants from gardens, shelter-belts or amenity plantations. Many are currently weakly naturalised; others are aggressive invaders. The invasion of *A. longifolia* subsp. *longifolia* and *A. longifolia* subsp. *sophorae* (Labill.) Court and their intermediates across southern Australia is causing the disruption of a broad range of vegetation communities including coastal vegetation, heathlands, woodlands and lowland-foothill forests (Carr *et al.* 1992, McMahon *et al.* 1996; Costello *et al.* 2000; Emeny *et al.* 2006) is cause for concern. Declines in floristic and faunal biodiversity (McMahon *et al.* 1996, Clay & Schneider 2000; Costello *et al.* 2000; Rees & Paull 2000) are associated with invasions of *A. longifolia*. The recent rapid expansion of *A. longifolia* populations in the Grampians, Victoria, a centre of extraordinary floristic richness, is of concern for biodiversity management. *Acacia longifolia* subsp. *longifolia* may not be indigenous to the Grampians (Entwisle *et al.* 1996), while *A. longifolia* subsp. *sophorae* is almost certainly an introduced taxon there. Intermediates between the two taxa complicate the invasion scenario and management prospects. The impact of widespread and intense wildfires during January 2006 on population trends of these acacias in the Grampians needs to be carefully monitored.

Invasion patterns

Bruzzese and Faithfull (2001) eloquently describe three principal invasion patterns of weedy native plants in Australia: disturbance responders, range extenders and new bioregion invaders. In summary, disturbance responders increase in density within their natural distribution, primarily due to changed management regimes. Range extenders increase their geographic distribution beyond the boundaries of their natural range; and new bioregion invaders include many species that have increased their range by transgression of large-scale geographical barriers e.g. deserts, mountain ranges or seas. I specifically refer to these plants as trans-continental invaders. The categories of invasion are not mutually exclusive, for example, a trans-continental invader such as *Leptospermum laevigatum* in Western Australia, is both a disturbance responder and range extender in eastern Australia, and conversely for the Western Australian species, *Acacia saligna*.

While biodiversity impacts are associated with each of the three classes of invasion, the more serious and intractable problems are usually associated with range extensions and invasions into new bioregions, particularly the latter where invaders often experience reduced herbivory pressure from phytophagous agents. Casual observations suggest this is the case for a broad range of invasive native plants including *A. longifolia, A. saligna, A. dealbata, A. pycnantha, L. laevigatum, Billardiera fusiformis* Labill., *B. heterophylla* (Lindl.) L. Cayzer, *Paraserianthes lophantha* (Willd.) I.C. Nielsen subspecies *lophantha* and *Hakea drupacea* (C.F. Gaertn.) Roem., perhaps contributing to their success as weeds, but quantified comparisons of host fitness and herbivory loads between indigenous and introduced distributions are sadly lacking.

Trans-continental native invaders seem to exhibit sigmoidal invasion curves, typical of many exotic invasive plants, indicating a release from biological or environmentally-induced constraints. Perhaps the best example of this is the colonisation and expansion of the Western Australian endemics *Billardiera heterophylla* and *B. fusiformis*, which are now scattered over large areas of eastern Australia (AVH 2006). In eastern Australia, these twining shrubs readily invade natural vegetation communities and can form dense, almost impenetrable thickets, clearly reducing biodiversity values and often limiting recreational and utilisation options for native vegetation. Native plant invaders that increase their range without transgressing large biological barriers (range extenders), are often accompanied by herbivorous agents, typically invertebrates that may limit the colonisation capacity and rate of spread of these weed species. An example of this is the presence of herbivores on *A. baileyana* in its invaded range in eastern Australia, which includes the seed-feeding curculionid *Melanterius maculatus* Lea, the flower-galling pteromalid *Perilampella ?hecateus*, flower and bud-galling cecidomyiids (*Asphondylia* and *Dasineura*

spp. (Adair *et al.* 2000), sap-sucking psyllids (Yen 2002) and a range of canopy-deforming fungi, including *Uromycladium notabile* McAlpine (Marks *et al.* 1982). These organisms can have a debilitating impact on the health of *A. baileyana* and all are likely to be indigenous in the host's natural range around Cootamundra, New South Wales, although movement of organisms from related acacias onto *A. baileyana* in its introduced range may also have occurred.

Fortunately, the vast majority of acacias currently in horticulture have not been recorded as naturalised, but methodologies designed to predict future invaders or safe taxa, for that matter, from this pool of species tend to be based on invasion histories or remain largely untested. It is difficult to visualise how risk assessment procedures, such as the analytical hierarchical process (AHP) (Weiss & McLaren 2002), could be sufficiently sensitive to predict new invasive acacia taxa, where many of the biological and ecological characteristics are so similar within the genus.

Control of invasive native plants

As invasive native plants are increasingly recognised as problematic in natural vegetation (Carr *et al.* 1992; Keighery 1999; Carr 2001; Groves 2001; Low 2001) many are subject to suppression programs to protect biodiversity values. Control options vary according to life-form, susceptibility, risk of non-target damage, ease of implementation, size of infestation and outcome targets. Control options for native plants include the use of herbicides, planned fire, grazing, manual removal, biological control, and integrated methods, including the highly effective method (for some woody plants) of 'rolling' infestations with heavy equipment, then burning after a period of drying (Muyt 2001). This paper focuses on the potential for biological control of Australian native plants, with a focus on Australian acacias.

Biological control

The concept of biological control of native plants in Australia commenced in 1901 with an augmentative

Figure 1. Distribution of Paraserianthes *lophantha* subsp. *lophantha* in Australia. A. indigenous range, B. naturalised range, although occurrences on the Furneaux Islands of Bass Straight may be indigenous (Harris 2001) and warrant investigation for clarification.

approach developed for the cosmopolitan perennial sedge *Cyperus rotundus* L. (Cyperaceae) by translocating the nut-grass coccid *Antonina australis* Green (Wilson 1960). This was followed in the 1990s by biocontrol of the disturbance-responders *Cassinia arcuata* R. Br., *C. laevis* R. Br. and *C. quinquefaria* R. Br. (Asteraceae) using native scale insects (Campbell & Wykes 1992; Holtkamp & Campbell 1995). Subsequent programs then targeted *Eremophila* spp. and *Dodonaea viscosa* Jacq. with the distribution of a coccid and eriophyiid, respectively (Sparkes & Robinson 1997; Sparkes 2000). More recently, the development of the classical biological approach for a range of native invasive plants is advocated including pathways for potential implementation (Adair 1995, Bruzzese & Faithfull 2001).

Eight species of Australian acacias are primary targets for classical biological control in South Africa using Australian organisms. After more than 30 years of research, in some cases, considerable success has been achieved in the biological suppression of *A. longifolia*, *A. cyclops*, *A. saligna*, *A. pycnantha* and *A. melanoxylon* R. Br. using a range of organisms including gall-

Table 2. Potential native plant targets (bold) for biological control in Western Australi

Feasibility	Ecological impact		
	High	Medium	Low
High	***Acacia dealbata, A. decurrens, A. langifalia, A. pycnantha, Leptaspermum laevigatum***	***A. baileyana, A. mearnsii, A. melanaxylon, A. flaribunda, A. podalyriifolia, Pittasparum undulatum***	*Acacia iteaphylla, A. elata, A. mallifolia, Brachychitan populneus, Hibiscus diversifalius, Acaena navae-zealandiae*
Medium	*Hydrilla verticillata*	*Melaleuca armillaris, Phragmites australis, Leptospermum ratundifalium*	*Bacopa monnieri, Callitris glaucophylla, C. columellaris, Casuarina* spp., *Dadanaea viscosa, Solanum aviculare, S. laciniatum*
Low		*Cyathea caaperi, Eucalyptus maculata, E. cladocalyx, Dennstaedtia davalliades, Hypalepis rugulosa, Vallisneria americana*[1]	*Aristida ramosa, Banksia canei, Eucalyptus* spp., *Juncus usitatus, Patamagetan crispus, Rumex brawnii*

[1]Current taxonomic revision of the genus may alter categorisation of this species.

Species in bold are priority targets, the remainder have a low probability for success or are unusable as targets

Table 3. Potential native plant targets (bold) for biological control in eastern Australia

Feasibility	Ecological impact		
	High	Medium	Low
High	***Billardiera heterophylla, B. fusifarmis***	***Acacia saligna, Hakea drupacea, Paraserianthes laphantha spp. laphantha***	*Aganis spp., Acacia cyclaps, A. iteaphylla, A. paradaxa, A. pulchella, A. pycnantha, A. rastellifera, Callistachys lancealatum, Dryandra farmasa*
Medium	*Hakea elliptica, Melaleuca diasmifolia*	*Hakea laurina, Melaleuca nesaphila*	*Callisteman rigidulus, Eucalyptus astringens, E. canferruminata, E. gomphocephala, E. kandinensis, E. accidentalis*
Low	*Melaleuca hypericifalia*		*Astartea heteranthera, Cladium procerum, Kennedia nigricans, Melaleuca incana, M. viminea*

Table 4. Potential biological control agents for native trans-continental invaders in Australia

Species	Common name	Target region	Family	Species	Mode of action	Conflict of interest[1]
Leptospermum laevigatum	Coast Tea-tree	WA	Cecidomyiidae	*Dasineura* sp. 1	Bud gall	L
			Cecidomyiidae	*Dasineura* sp. 2	Bud gall	L
			Gracillariidae	*Parectopa thalassias*	Leaf miner	M
			Coccidae	Undetermined	Sap sucker	H
			?Eriophyiidae	Undetermined	Twig deformer	M
Acacia longifolia	Long-leaf Wattle	WA	Pteromalidae	*Trichilogaster acaciaelongifoliae*	Shoot gall	M-H
			Curculionidae	*Melanterius ventralis*	Seed feeder	L
			Cecidomyiidae	*Dasineura acaciaelongifoliae*	Flower gall	L
Acacia dealbata	Silver Wattle	WA	Curculionidae	*Melanterius maculatus*	Seed feeder	L
			Pteromalidae	*Perilampella ?hecateus*	Flower bud gall	M
			Cecidomyiidae	*Dasineura pilifera*	Flower gall	L
			Cecidomyiidae	*Dasineura sp. nov.*	Pouch gall	L
			Pteromalidae	Undetermined	Leaf rachis gall	L
			Uredinales	*Uromycladium tepperianum* (biotype)	Stem/leaf/flower gall	H
			Cecidomyiidae	?*Cecidomyia* sp.	Flower gall (Red Plush Gall)	L
Acacia decurrens	Green Wattle	WA	Cecidomyiidae	*Dasineura pilifera*	Flower gall	L
			Curculionidae	*Melanterius maculatus*	Seed feeder	L
			Uredinales	*Uromycladium tepperianum* (biotype)	Stem/leaf/flower gall	H
Acacia mearnsii	Black Wattle	WA	Curculionidae	*Melanterius maculatus*	Seed feeder	L
			Cecidomyiidae	*Dasineura rubifarmis*	Flower gall	L
			Cecidomyiidae	*Dasineura sp. nov.*	Flower gall	L
			Cecidomyiidae	*Dasineura fistulosa*	Flower gall	L
			Cecidomyiidae	*Asphondylia* sp.	Bud gall	L
			Uredinales	*Uromycladium tepperianum* (biotype)	Stem/leaf/flower gall	H

Species	Common Name	Target Region	Family	Species	Mode of Action	Conflict of Interest[1]
Acacia melanoxylon	Blackwood	WA	Curculionidae Cecidomyiidae	*Melanterius acaciae* *Dasineura furcata*	Seed feeder Flower galler	L L
Acacia pycnantha	Golden Wattle	WA	Pteromalidae Uredinales	*Trichilogaster signiventris* *Uromycladium tepperianum* (biotype)	Shoot galler Stem/leaf/flower galler	M H
Acacia podalyriifolia	Mount Morgan Wattle	WA	Eurytomidae	*Bruchophagus* sp.	Seed feeder	L
Pittosporum undulatum	Sweet Pittosporum	WA	Agromyzidae Phlaeothripidae Chrysomelidae Psyllidae Cerambycidae	*Phytoliriomyza pittosporophylli* *Teuchothrips pittosporicola* *Lamprolina aeneipennis* *Trioza viteoradiata* *Strongylurus thoracicus*	Leaf miner Sap sucker Defoliator Sap sucker Wood borer	M M M M M
Billardiera heterophylla, B. fusiformis	Blue-bell Creeper	VIC, SA,TAS, ACT	Cecidomyiidae Cecidomyiidae ?Eriophyiidae	*Asphondylia* sp. ?*Lasioptera* sp. Undetermined	Bud/shoot galler Shoot-tip galler Stem deformer	M M H
Acacia saligna	Port Jackson Wattle	VIC, NSW	Curculionidae Uredinales Eriophyiidae	*Melanterius compactus* *Uromycladium tepperianum* (biotype) *Aceria acaciflaris* *Aceria burnleyae*	Seed feeder Stem/leaf/flower galler Shoot deformer Inflorescence deformer	L H M
Paraserianthes lophantha subspecies *lophantha*	Cape Leeuwin Wattle	VIC, TAS, NSW	Curculionidae Uredinales	*Melanterius servulus* (biotype) *Uromycladium tepperianum* (biotype)	Seed feeder Stem galler	L M
Hakea drupacea	Sweet Hakea	VIC, TAS, NSW	Cerambycidae	*Aphanasperma* sp.	Seed Feeder	?L
Acacia cyclops	Red-eye Wattle	VIC, SA	Curculionidae Cecidomyiidae Cecidomyiidae	*Melanterius servulus* *Dasineura dielsi* *Asphondylia* sp.	Seed feeder Flower galler Bud galler	L L L

[1] H= high risk of conflict of interest, M= medium risk, L= low risk.

forming cecidomyiids and pteromalids, seed-feeding curculionids, and a gall-inducing pathogen (Olckers & Hill 1999). The accumulation of knowledge on the biology and taxonomy of organisms associated with Australian acacias through biological control programs has been of considerable mutual benefit to both South Africa and Australia, where the legacy is contributing to better natural resource management. Other nations, such as Portugal, now plan the implementation of biological control of Australian acacias (Sheppard *et al.* 2006).

In Australia, invasive native acacias are not subject to intentional biological control. However, in the case of trans-continental invaders, where natural and introduced populations are separated by large and often hostile geographical barriers, there is potential for the utilisation of classical biological control principles to develop suitable control programs. Australian acacias often support rich phytophagous biotas (New 1984), with many species exhibiting high levels of host specificity (Kolesik *et al.* 2005, Yen 2002), a mandatory requirement for acceptable biocontrol. Those organisms that are also capable of disrupting growth or reproductive patterns and themselves are constrained by similar geographical barriers as their host, are candidates for biological control within Australia. As natural enemies (parasitoids, predators and pathogens) frequently influence the ecology of phytophagous organisms on native plants, the introduction of phytophagous organisms across biological barriers without their specialist natural enemies may accrue population increases of the phytophage in the introduced range by the creation of enemy-free or enemy-reduced space, thus contributing to the suppression of the target weed. However, several factors could mitigate against the success of such an approach. Australian acacias appear to vary considerably in the richness of their phytophagous biota, with some species apparently supporting meagre faunas, therefore offering limited opportunities for the selection of potential biocontrol agents. Natural enemies with broad geographical distributions could handicap the creation of enemy-free space in the introduced range of invasive plants and prevent the build-up of super-populations of the selected phytophage. In addition, the progressive range extension of invasive native plants can reduce the distance between indigenous and introduced distributions, weakening biological barriers (e.g. figure 1), therefore increasing the potential for natural enemies to undertake trans-continental dispersal, via the colonisation of naturalised or ornamental populations of the host into the main invasion zone. Furthermore, with readily accessible domestic travel routes within Australia and high trans-continental movement rates, the risk of accidental or deliberate movement of natural enemies associated with biological control agents for native plants would be higher within Australia compared to biocontrol programs operating overseas.

Invasion of eastern Australian cecidomyiids in Western Australia - proof of concept

The gall-forming cecidomyiid *Dasineura rubiformis* Kolesik is restricted to a small group of *Acacia s.s.* section *Botrycephalae* species indigenous to eastern Australia, with *A. mearnsii* De Wild. as the principal host (Kolesik *et al.* 2005). Eggs are laid on or around the ovary of open flowers, which soon become swollen and distorted forming small basal chambers used for larval development. Affected ovaries fail to produce seeds. Larvae remain within the gall until June-August then emerge to pupate in the soil beneath the host tree. Adults emerge at the onset of flowering in September-November and are very short lived. In eastern Australia, the insect is mostly heavily parasitised by micro-hymenoptera and gall densities are usually low, sporadic and have little impact on overall fruit production. This is in contrast to populations in Western Australia, where super abundant densities are common, widespread and appear regularly on *A. mearnsii*. This is largely attributed to reduced parasitoid pressures (Adair 2004). In Western Australia, *A. mearnsii* is non-indigenous and weakly invasive. Entomological surveys on *A. mearnsii* and other acacias in Western Australia by South African scientists in the 1980s did not detect the presence of *D. rubiformis* (M. van den Berg unpublished data), suggesting that colonisation occurred post-1980, but the exact date and mode of entry into Western Australia cannot be determined. Super-galling by *D. rubiformis* significantly reduces seed production of *A. mearnsii* in Western Australia (Adair 2004) and undoubtedly contributes to the suppression of this plant in the south-west region. As no indigenous Western Australian acacias are hosts to *D. rubiformis*, the insect is an exemplary

case of the potential for biological control of invasive trans-continental plants. Two other eastern Australian cecidomyiids, *D. pilifera* Kolesik and *Dasineura* sp. (Pouch Galler), occur on *A. dealbata, A. decurrens* and *A. baileyana* in Western Australia and while density levels appear to be relatively low, no data are available on population trends to determine likely impacts of these insects.

Selection of native plants as targets and implementation of biological control

Classical biological control techniques mostly require substantial investment of resources and human effort (Harley & Forno 1992). Accordingly, targets selected for biological control require favourable cost:benefit ratios and reasonable probabilities of success, and should be directed at invasive species that cause, or have the potential to cause, serious ecological or economic harm. While quantitative data are absent for all of these criteria for native invasive plants, prospective biocontrol targets can be identified using a qualitative assessment process. This assessment would be based firstly on characteristics of the plant: invasiveness, disruption to ecological processes, impact on biodiversity values, and rate of spread. Secondly, the potential for success based on availability of host specific organisms and their likely impact, the degree of bio-geographic segregation in the introduced range, and the potential for conflict of interest would be taken into account. Using the process outlined above, potentially suitable targets for biological control have been identified: 11 species in Western Australia (table 2) and five species in eastern Australia (table 3). The absence of indigenous *Botrycephalae* in Western Australia contributes substantially to their suitability as targets for biocontrol in that state. In addition, as most Western Australian acacias are medium to small shrubs, and rarely trees, invasive *Botrycephalae* are likely to have profound ecological impacts in natural ecosystems, therefore further increasing their suitability as biocontrol targets.

Fortuitously, the phytophagous faunas associated with many Australian trans-continental invaders have been documented to varying degrees, largely the result of biocontrol prospecting undertaken by South African biologists (van den Berg 1978, 1979, 1980a,b,c, 1982a,b,c; unpublished data). Therefore, potential biocontrol agents can be identified and the level of potential conflict of interest assessed based on mode of feeding of the respective agent (table 4). However, for several invaders, namely *Hakea drupacea, Acacia floribunda* (Vent.) Willd. and *Acacia podalyriifolia* Cunn. ex Don, few phytophagous records are available and exploratory work is required to identify potential agents for these species.

Australian horticultural industries utilise native trans-continental invasive plants, mostly as ornamental plants for domestic or international trade, therefore attempts to undertake biological control could establish conflicts of interest with these industries and their clients. Procedures for resolving conflicts of interest associated with the introduction of biological control agents are available through the *Biological Control Act* 1984 (BCA). The BCA was developed to deal with organisms exotic to Australia, but it could also be applied to native organisms, although this remains untested. In situations where the target plant has no economic value or where the potential agent generates low and resolvable levels of conflict, formal use of the BCA may not be required, a desirable outcome as utilisation of the BCA can incur considerable costs (McLaren *et al.* 2006). Many of the conflicts of interest potentially associated with biological control of Australian native plant invaders could be resolved by declaration of the invader under State or Territory noxious weed legislation, even if the declaration only restricts the sale, transport or trade of the listed species. Currently, few Australian native plants (*Acacia baileyana, A. paradoxa, Cassinia arcuata, Ceratophyllum demersum* L., *Hydrilla veriticillata* (L.f.) Royle, *Pittosporum undulatum, Sclerolaena birchii* (F. Muell.) Domin, *Typha* spp.) are declared as weeds (Thorpe & Wilson 2006) on the basis of their ecological damage. The development of case studies to explore the natural enemy complexes of native invasive plants in the context of development of biological control is advocated (Bruzzese & Faithfull 2001). An additional advantage of such an approach would be to explore the legislative frameworks and procedures that would enable the development of classical biological control of Australia's trans-continental invaders. This important process would include development of protocols for host specificity testing and evaluation of results. The suggestion of *Billardiera* (*Sollya*) *heterophylla* and *L.*

laevigatum as candidate species (Bruzzese & Faithfull 2001) for biological control is considered the only plausible method for landscape-scale suppression of these weeds. However, the invasive *Acacia* species identified in this paper should also be considered. Collaborative research arrangements between relevant Western Australian and eastern Australian government authorities, under the auspices of the Australian Weeds Committee, could expedite the development of this concept.

Future trends

The demand for horticultural novelties contributes to the introduction of new native plants into Australian horticulture. The rate of plant naturalisations in Australia is increasing (Groves 1997) and current trends suggest that more Australian native plant species will establish as problematic environmental weeds. The adoption of early intervention control strategies could help alleviate this scenario, if native plants are taken into consideration as potentially problematic weeds. However, careful consideration to the native plant species utilised by Australian horticultural industries could contribute even more to the prevention of new and emerging weedy native plants. While our ability to predict new weeds with no previous invasion history is weak, a precautionary approach to the adoption and promotion of non-indigenous native plants should be supported. The same principle needs to be applied to the promotion of Australian plants, particularly acacias, in overseas markets, where the global distribution of species for fodder, fuel, fibre and timber, particularly in less developed countries, may ultimately cause problems worse than those they were intended to solve.

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Australian acacias as multi-purpose agro-forestry species for semi-arid regions of Africa

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Introduction

Human populations living in semi-arid regions of the developing, tropical world who are reliant on annual crops and/or pastures (for livestock) for food are particularly vulnerable to hunger and periodic famine. Certain Australian *Acacia* species have great, untapped potential as multi-purpose tree species in agro-forestry systems in these regions. A number of species thrive under conditions which annual plants struggle to survive in. Uses include planting for windbreaks, reclamation of degraded land, biomass production for mulch and organic matter, firewood, feed for honey bees, and food for humans and livestock.

The real problem of rain-fed agriculture: drought or farming practices?

News headlines announcing famine in Africa are tragically all too common. Though the exact country or region impacted by famine may vary from year to year, more often than not, crop failure and subsequent famine are related to drought. Media releases and reports from aid and government agencies often express surprise that drought has occurred again even in climatic zones where one should expect drought to be a regular feature of the climate. Thus, even in semi-arid zones, analysts have tended to treat drought as an anomaly and people relying on annual crops in these regions regularly experience drought-induced crop failure. While the significant impact drought has on crop yield and subsequent famine cannot be ignored, drought itself is not as big a contributor to famine as the actual farming practices of people living in arid and semi-arid regions.

Two features of many African farming systems in particular increase vulnerability to crop failure:

- lack of biodiversity. Farming systems are dominated by a narrow range of annual crop species. Often farmers rely primarily on a single annual crop such as maize, millet or sorghum in a highly risky environment. If this crop is damaged through drought, pests or other adverse factors, subsistence farmers have little else to fall back on and famine can ensue.

Abstract

The seeds of certain Australian *Acacia* species are tasty, safe to consume and nutritious. Being perennial, mature acacias can take advantage of rains that would be ineffective for annual crops, such as out of season or poorly distributed rains. *Acacia* seeds are easily harvested and processed into flour using simple technologies which already exist in typical African villages. The flour can be incorporated into local dishes and "non-traditional" foods such as spaghetti, bread and biscuits. The seed also has great potential as livestock feed. Alternatively, the hard-coated seeds can be easily stored for many years and act as a famine reserve food.

Much effort has gone into safety testing and promoting edible seeded Australian acacias for direct human consumption, but the rate of adoption has been slow. However, other characteristics of these same species may have an even greater impact on food security than actual consumption of the seed. The Farmer Managed Agro-forestry Farming System (FMAFS) that incorporates a range of annual and perennial crops is being promoted as a sustainable rainfed farming alternative to traditional and destructive slash-and-burn monocultures.

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- absence of ground cover and low soil organic matter content. Farming methods commonly practiced involve the complete removal or destruction of crop residue through burning. Regular turning of the soil under hot tropical conditions hastens the rate of loss of organic matter. In highly degraded environments, where there is a shortage of fire wood and fodder, crop residues are removed from fields for use as cooking fuel or for animal fodder. With no mulch covering the soil, heavy downpours result in high levels of water runoff and soil erosion, high evaporation rates and low water infiltration rates. Bare soils are also exposed to higher temperatures than covered soils which adversely effects germination and the growth of juvenile plants (Ashraf *et al.* 2004). Bare soil surface temperatures measured at the start of the rainy season in fields near Maradi, Niger Republic, reached 50°C, whereas number of days to 50% germination of millet decreases due to high temperatures (45 °C) (measured by author). Soil organic matter also helps improve soil structure and increases water and nutrient holding capacity.

Conversely, unpublished field measurements undertaken by the Maradi Integrated Development Project (MIDP) in Niger Republic showed at least a doubling of crop yield and significant increases in income, and ensured annual minimum production levels despite variable conditions, have been attained through increasing biodiversity and returning organic matter to the soil (Pasternak *et al.* 2003).

Promotion and use of Australian acacias for human nutrition

Australian edible seeded acacias have great potential for combating hunger in semi-arid lands (Rinaudo *et al.* 2002). A number of species thrive under conditions which are adverse for common annual crops such as millet and sorghum. Growth and yield performance of such annuals can be compromised by high soil temperatures at planting time, strong winds causing abrasion of leaf surfaces and desiccation, inadequate or untimely rains, or outright burial by sand. Whereas annual crops must be planted each year and so face these risks annually, acacia trees live for many years after establishment and are resilient to high temperatures and strong winds. *Acacia* species trialled in Niger have extensive root systems and other drought coping strategies and being perennial, they are able to take advantage of untimely rains. These include species such as *A. colei* Maslin & L. A. J. Thomson *var. ileocarpa* M.W. McDonald & Maslin, *A. coriacea* DC. *sens lat.* (including *A. sericophylla* F.Muell.), *A. elachantha* Maslin & M. W.McDonald, *A. torulosa* Benth., *A. tumida* F. Muell. ex Benth. var. *tumida*, *A. tumida* var. *kulparn* M. W. McDonald, and *A. victoriae* Benth. *sens lat.* (subspecies unknown). The seeds of these species are tasty, safe to consume and nutritious, having a protein, carbohydrate and fat content of 17-25%, 30-40% and 14-16% respectively (Brand and Cherikoff 1985). In many regions, such as West Africa, the seeds ripen at a time of low labour demand when non-irrigated crops are not being cultivated. Being perennial and thus having established root systems, mature acacias can take advantage of rains that would be ineffective for annual crops (e.g. out of season or poorly distributed rains). *Acacia* seeds are easily harvested and processed into flour using simple and existing local technologies. The flour can be incorporated into local dishes and in "non-traditional" foods such as spaghetti, bread and biscuits. The seed also has great potential as a food supplement for livestock. Alternatively, the hard-coated seeds can easily be stored for many years so give flexibility with timing of use and can act as a famine reserve food. *Acacia* species can also supply various other products, especially fuel wood, and services such as improvement of soil fertility through fixation of atmospheric nitrogen.

With the technical assistance of the Australian Tree Seed Centre, *Acacia* species trials were commenced in the Maradi region of Niger in 1992 by the Maradi Integrated Development Project (MIDP). During the famine of 1994, MIDP facilitated the planting of over 100,000 *Acacia* trees and promoted the utilization of the seeds for food. Since 1994, MIDP staff have continued to promote *Acacia* planting and use in the Maradi Department. Despite these concerted efforts, adoption of *Acacia* seed into human diets in Niger has been slow, although a number of individuals and in some cases, whole villages in the Maradi area are consuming *Acacia* seed regularly (Abasse & Yahaya, pers. comm.).

In light of Niger's chronic food shortages and recurrent famines, the slow adoption rates have been both surprising and disappointing. The lack of market demand for seed for consumption both locally and abroad has also resulted in a general lack of interest in planting and cultivating acacias. It is now felt that in order for the farmers to become interested in planting acacias, and in the absence of a significant market for seed, focus has now moved from promotion for direct human consumption alone to promotion of the multiple benefits acacias offer.

Farmer managed agro-forestry farming system

In continuing to explore how acacias can be best promoted and utilised, MIDP staff are developing the Farmer Managed Agroforestry Farming System (FMAFS). FMAFS is an alley-cropping, agro-pastoral forestry system which incorporates a wide range of annual and perennial, and indigenous and exotic plant species and livestock. While the FMAFS is being introduced as a model, actual layout and choice of tree numbers and types of indigenous and exotic trees and annual crops is determined by farmers themselves. However, a major recommendation to FMAFS implementers is that acacias be widely spaced on the boundary and within the farm. FMAFS introduces a range of high yielding seed and wood producing Australian acacias (*A. colei, A. torulosa, A. tumida, A. elachantha*) which are planted along farm borders and in rows within the farm and provide human and animal food, services of environmental restoration and crop protection, firewood, timber and mulch.

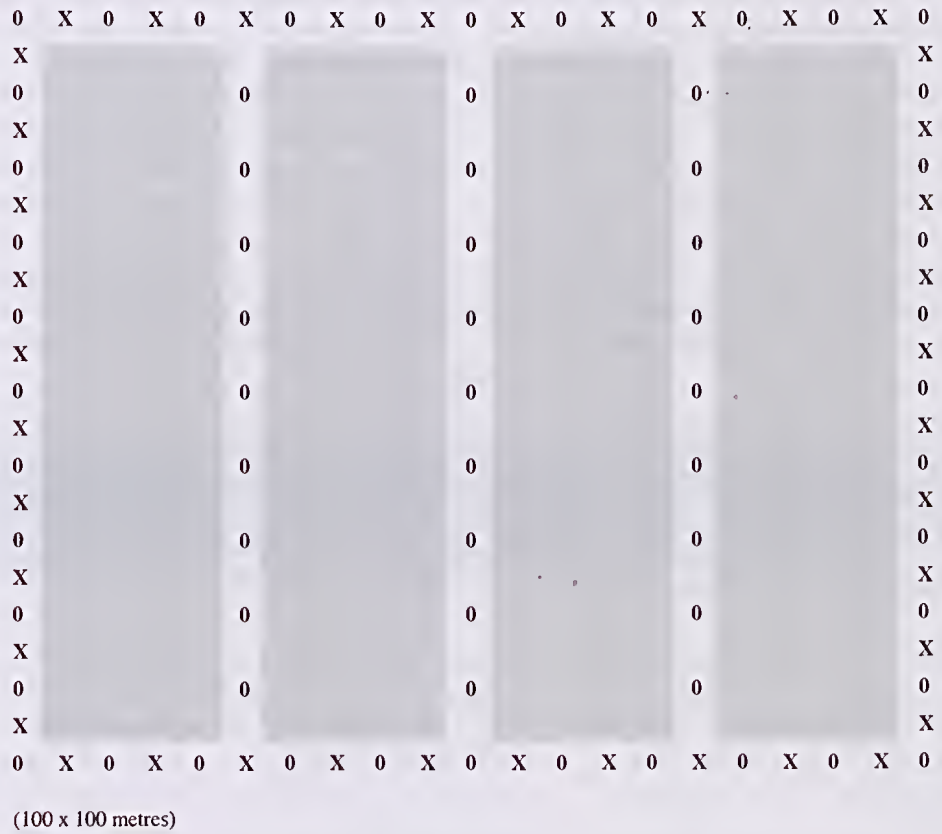

Figure 1. The Farmer Managed Agroforestry Farming System, one hectare model. 0= *Acacia colei* (68), X= *Acacia torulosa* (40): Total acacia trees 107 per ha. Trees on boundary are 5m apart. Trees within the farm are 10m apart. Rows of trees are 25m apart. Rows of trees are planted across the prevailing wind direction. Shaded area: FMNR with 40 to 120 trees per ha and annual/perennial crops in rotation.

Including more than one species of *Acacia* increases the likelihood of realising a seed harvest each year. Other valuable agroforestry trees such as *Pomme du Sahel* (*Ziziphus mauritiana* Lam.), Tamarind (*Tamarindus indica* L.), Baobab (*Adansonia digitata* L.) and Moringa (*Moringa oleifera* Lam.) complement regenerated indigenous trees and acacias. Annual cash crops such as millet, sorghum, cowpeas, peanuts, hibiscus, sesame and cassava can then be planted in rotation between the tree rows, providing food and fodder and income while crop residues are used as mulch for soil improvement and protection. FMAFS provides a diversity of income sources, and enables a better distribution of farm labour and income throughout the year. With FMAFS, farm income is increased significantly compared to traditional millet farming.

The *Acacia* trees are planted on the farm borders at five metre intervals and in rows 25 metres apart with trees within the row 10 metres apart. Rows of trees are planted across the prevailing wind direction. Various models have been designed to suit varying sites. The one hectare model (Figure 1) has 107 acacia trees per hectare and half hectare models have between 69 – 72 trees. The *Acacia* trees are pruned every second year and produce edible seed every year from the second year after planting. As seed yields vary considerably between trees and from year to year (Table 1), cultivar selection trials are being conducted by MIDP to identify superior trees and to generate stable high-performing cultivars.

Acacia trees are planted at wide spacing on farm borders to allow high seed and wood yields and in order to minimise competition with crops. Pruning is undertaken every second year in order to maximise seed production. While branches and phyllodes pruned from acacias provide mulch, the bulk of the mulch in FMAFS comes from crop residues and pruning of indigenous species.

FMAFS addresses the principal contributors of vulnerability to food insecurity, namely lack of biodiversity, absence of ground cover and low soil organic matter content. Thus implementation of FMAFS results in shifting from reliance on an annual species monoculture to spreading risks through maximising biodiversity and incorporation of perennial indigenous and exotic species into the cropping equation. This shift provides alternate income sources and greater insurance against total crop loss during adverse events such as drought or insect attack. Not all species will be equally disadvantaged by the same adverse event in a particular year. In a biologically diverse farming system, there will be an assured minimum income in any year. The Australian acacias' high tolerance to drought (Cossalter 1987) and lack of susceptibility to most African crop pests and diseases make them an excellent backstop for seasons when annual crops fail. The *Acacia* species planted in Niger come from Australia's subtropical dry zone which receives less than 500 mm of rainfall per

Table 1. Seed and wood production from four year old *A. torulosa* trees grown on field borders. Danja, Niger Republic (Cunningham & Abasse 2004).

Tree type/ Number	Mean weight of pods and seed (kg)	Mean weight of pods (kg)	Mean weight of seed (kg)	Dry weight of wood (kg)
Branching types (39)	9.7	5.4	4.0	
Branching types (25)	12.5	7.0	5.2	
Tall types (19)	4.9	2.4	1.7	
Branching tree No. 222	27.0	14.0	12.0	117.0
Branching tree No. 241	21.0	13.0	7.5	30.0
Branching tree No. 62	18.0	9.0	7.7	14.0
Tall tree No. 313	12.0	5.0	3.5	49.0
Tall tree No. 300	8.0	4.0	3.5	25.0
Tall tree No. 305	8.0	4.0	3.0	38.0

Column one: (Tree type / number) is the category of trees or tree. The number in brackets is the number of trees. For example, branching types (39), means that 39 branching trees were selected and the data in other columns is the mean of these 39 trees. All the other categories are the data for individual trees (i.e. Branching tree no 222 gave 14 kg pods, etc.)

annum. Acacias are growing under harsh conditions in Niger, in areas receiving as little as 200 mm of rainfall, with the dry season lasting at least eight months and temperatures often exceeding 40°C. In the 20 years that Australian acacias have been grown in Maradi, no serious or sustained insect attack or diseases have been reported. In 2007, hairy caterpillars (species unknown) caused some damage on newly planted trees and required spraying. These caterpillars do not appear in plague proportions every year. Die-back, perhaps caused by a fungus, has been noted to affect *A. colei* in some years but this has not posed major problems. Even in high rainfall years, crop yields and incomes are increased by intercropping with acacias for a number of reasons. Few farmers in Niger can afford to buy pesticides or artificial fertiliser, and organic matter is in short supply. Pests can reach plague proportions quickly in the absence of artificial or natural controls and soils are very infertile. Having trees in fields provides food, shelter, habitat and vantage points for natural pest predators. Over time, acacias contribute nitrogen and organic matter to soils, positively impacting millet yields. Even in good years, wind speeds at planting time can reach up to 70 km per hour, devastating emerging crops in the absence of wind breaks.

Implementation of FMAFS also results in the production of biomass by both acacias and indigenous species, providing mulch, organic matter, a wind-break effect and fuel for firewood and income generation. Soils in Niger are extremely infertile and average per hectare fertiliser use is only 5 kilograms. Consequently, average millet yields under traditional cultivation techniques are only in the order of 300 kg per hectare. Mulching increases soil fertility, enhances moisture infiltration and retention significantly and reduces soil temperatures. The large quantity of biomass laid down as mulch results in millet yield increases of 100% or more over untreated plots (unpublished MIDP data). The rainy season in Niger only lasts for four months and is very variable and erratic. Under traditional farming systems, millet is grown during the rainy season in fields completely cleared of trees. Millet stalks constitute low quality fodder and very few grasses or edible weeds grow in the fields during the eight-month dry season. Under FMAFS, many indigenous trees left in fields produce edible pods and leaves which attract livestock. In addition to leaf litter fall contributing to soil organic matter, livestock spend more time seeking pods and leaves from trees and therefore deposit more manure in treed fields than in non-treed fields.

FMAFS is flexible enough to meet farmers varying needs and priorities as it is not prescriptive. FMAFS builds on the strengths of two existing agroforestry systems, the Sahel Eco Farm model (Pasternak *et al.* 2005) and Farmer Managed Natural Regeneration (FMNR) (Rinaudo 2001), which have also been developed in Niger Republic (Appendix I).

Adoption of innovation can be very slow. Building on the success of FMNR and on farmers' existing knowledge is important. Though now widely practiced, FMNR initially met with strong resistance from communities in which it was a tradition to clear all trees from cropland. Nigerien farmers have now had up to 20 years of experience growing indigenous trees on crop land and are familiar with the benefits and the various management options open to them. Introducing FMAFS to farmers already practicing FMNR requires only a relatively small adjustment in thinking and involves a slight increase in complexity. Farmers practicing FMNR have already made a significant paradigm shift in moving from mono-cropping of annuals to agroforestry. Good reasons for building on FMNR include:

- FMAFS represents an incremental graduation into a slightly more complex farming system, but one which offers increased benefits and a reduction in vulnerability to famine. Through FMNR, farmers' deep prejudice against having trees on fields has already been overcome and this knowledge base can be built on.
- Through FMNR, most farmers' fields in Southern Niger are already covered with a diversity of trees which contribute to land restoration and provide food, medicines, firewood, timber and rope and enhanced crop and livestock production.
- FMNR has a low labour requirement, is cheap and easy to implement, and gives multiple benefits quickly. These characteristics have resulted in FMNR spreading across Niger largely by word of mouth, from farmer to farmer in contrast to high external input initiatives which are entirely dependant on the presence of a project manager and external funding.

Progress to date

MIDP has been promoting edible-seeded acacias since 1994 and World Vision, with technical assistance from MIDP has been involved since 2004. In 2006, following formation of ten village farmers groups, 15 to 25 selected farmers per village established 125 FMAFS plots. In 2007 there have been 253 new FMAFS established in 33 villages in the Maradi area. As interest grows, ongoing discussions and evaluation of the work to date will further inform how FMAFS will be tailored to meet farmers changing needs.

Conclusion

Multi-purpose Australian acacias are poised to make a significant contribution to food security in semi-arid regions of Africa; regions with a history of recurring food shortages. The Farmer Managed Agroforestry Farming System provides a good vehicle for the rapid spread and adoption of this model because of its flexibility, simplicity, low dependence on external inputs, low cost and ease of replication by farmers themselves.

Cautionary note

The Australian species mentioned in this article have not become weeds under the high livestock pressure, high wood demand and harsh environment of West Africa. However, being pioneering species, caution needs to be exercised when introducing acacias into new regions. National regulations for introducing exotic species should be obeyed. Project managers should consult Departments of Agriculture and Forestry and other historical records on plant introductions before proceeding. Once authorisation has been obtained, testing should be undertaken in collaboration with the appropriate government department only on well controlled and managed sites. Contingency and eradication plans should be in place from the outset if weediness tendencies are noted.

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Appendix I

Sahelian Eco-farm

The Sahelian Eco-farm (SEF) is an alley cropping system under development at ICRISAT Sahelian Centre (Niger), in which trees and/or shrubs are intercropped with annual crops. The first SEF model under development is composed of *Acacia colei*, *Ziziphus mauritiana* and three annual crops (millet, cowpeas and Roselle). Erosion by wind is prevented by the wind breaking effect of the *A. colei* trees and by mulch produced from the *Acacia* branches and phyllodes. *Acacia colei* trees play a major role in soil fertility enhancement. The trees are pruned once a year and their branches are spread over the field adding organic matter to the soil. Tree roots add organic matter and fix atmospheric nitrogen. Soil fertility is also enhanced by crop rotation. *Acacia* seeds are used in poultry feed. It is estimated that the combined profit per ha from all the SEF components is ten times higher than the profit derived from a millet field. SEF addresses the main constraints of Africa's rain fed agriculture, namely soil erosion, low soil fertility, low water use efficiency, drought, shortages of animal fodder, low income and an inefficient distribution of the labour force throughout the year.

Farmer-Managed Natural Regeneration

Farmer-managed Natural Regeneration (FMNR) is a rapid, cost effective method of re-establishing tree and woody shrub cover in forestry and agro-forestry production systems. It involves farmers managing coppice shoots from pre-existing stumps and natural seedling regeneration, especially of useful woody species. In most cases neither guarding nor fencing are employed to protect new growth. Shoots pruned at the start of the rainy season when crops are growing in the fields have five months to grow without interference from livestock. After this time some damage may be incurred but trees generally are able to grow large enough to not be destroyed by livestock. Of greater importance for the survival of the trees is agreement by all stakeholders to respect each others property.

Its direct benefits include:

- increased availability and use of firewood and building timber;
- increased incomes from sale of wood and tree products; and
- improved human nutrition associated with a more diverse and healthy diet (incorporating edible leaves, seeds, nuts and fruits).
- higher annual crop yields grown in FMNR treated fields through environmental protection (reduced wind and soil erosion), improved soil fertility and water-holding capacity,
- improved livestock productivity through better nutrition (as a result of increased availability of tree fodder in the dry season).

Since FMNR was introduced into Niger in 1983, the practice has spread to at least 3 million hectares of previously denuded farmers land (Larwanou *et al.* 2006) in Niger Republic.

Reproductive biology and germplasm evaluation of *Acacia nilotica* (Linn.) Willd. ex Del. from North India

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Abstract

Acocia nilotico exhibits morphogenetic diversity in the form of three North West Indian varieties, namely, var. *typica*, var. *kaurio* and var. *cupressiformis*. These are distinguishable on the basis of bole, crown, spine and pod characters. The present communication covers the observations on the reproductive biology and germplasm evaluation in these varieties. In spite of having ca 1/3-1.2 of flowers pre head with sterile pistils, trees produce numerous pods, and seeds per pod. Trees of var. *typico* from dry zones provide the best wood both as timber and fuelwood. For bark tans, older trees over 40 years of var. *typica* should be harvested. Gum yield is the highest in var. *cupressiformis* but var. *typico* produces superior quality gum. On the basis of various fodder characteristics and *in vitro* dry matter digestibility (IVDMD), var. *typico* produces the best quality fodder both as leaf and pod. For the majority of the economic attributes, var. *typica* is far superior to var. *kourio* and var. *cupressiformis*.

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Introduction

Acacia nilotico (Linn.) Willd. ex Del. is very widely distributed in the arid and semi-arid regions of India. It forms extensive and generally pure forests, locally referred to under different names in different states of India as *Babul Savannah*, *Acacio Forests*, *Inundotion Bobul Forests*, *Bobul Bans*, *Babul Meodows*, *Desert Thorn Forests*, or *Rovine Thorn Forests*, etc. Outside India, it grows well in subtropical to tropical regions of Asia, Africa, Australia and Caribbean. The species exhibits considerable morphogenetic variability in the form of different varieties/sub-species. Worldwide, 9 subspecies and 3 varieties (Brenan 1983) or 10 subspecies and 2 varieties are known to exist which show intensive hybridization among themselves. The species has a wide morphogenetic base and seems to constitute a complex with diploid (2n=26), tetraploid (2n=52), octoploid (2n=104) and 16-ploid (2n=208) cytotypes besides some aneuploid chromosome numbers, 2n=24, 44, 48. Three varieties, var. *typico*, var. *kauria* and var. *cupressiformis* detected by the authors in North West Indian taxa, can be easily identified in the field on the basis of their bole, crown, spine, leaf and pod characteristics (Singhal & Kaur 2004).

Acocia nilotico is one of the best multipurpose tree (MPT) species providing 1st class commercial timber (Pearson & Brown 1932), excellent ash free fuelwood with high calorific value (Krishna & Ramaswamy 1932; Trotter 1940; Pathak 1993), best quality charcoal (Patil *et al.* 2000), good fodder as leaf and pod (Singh 1982), quality gum (Dwivedi 1993), and a high percentage of bark tannins (Dwivedi 1993). Besides, the species is of considerable importance in agro-forestry and wasteland management for its ability to grow fast and fix atmospheric nitrogen. As a pre-requisite it is desirable to evaluate the morphogenetic diversity in the species with respect to various attributes of economic utility on variety basis. Various aspects of flowering phenology, floral biology, pollination mechanism and compatibility behaviour at variety level are also required in order to understand the breeding system of the species. Keeping in view its importance and wide morphogenetic base, different aspects of reproductive biology are essential to understand the breeding system. The present communication covers the reproductive biology and

germplasm evaluation of three varieties for North West India where these varieties are well distributed.

Material and Methods

To study reproductive biology and germplasm evaluation, seventy accessions belonging to var. *typica*, var. *kauria*, and var. *cupressiformis* were selected from the dry, semi-dry and sub-mountainous regions growing in the states of Punjab, Haryana, Himachal Pradesh, Uttar Pradesh, Uttranchal and Rajasthan (Table 1). The sample trees were screened for chromosome number, microsporogenesis, and pollen and seed fertility. Phenological observations for initiation of leaf and inflorescence primordia, time of peak blooming, and decline in flowering, were made from the marked individuals. For flower development, marked floral heads were observed at one day intervals for 50–60 days. Flower structure is based on wide sampling of 20–25 flowers per head in each variety. Time of anthesis, anther dehiscence and stigmatic receptivity was determined by observing the marked heads at 1 hour intervals. Healthy, glistening white and shining surfaced stigmas were considered as apparently receptive, while dull, pale coloured and shrivelled ones were assumed non-receptive. Pollen fertility was determined through the glycerol-acetocarmine mixture (1:1) and tetrazolium chloride (1%) staining method (Shivana & Rangaswamy 1992). Actual pollen viability was estimated by germinating pollen on a 1% agar medium supplemented with 10–12% sucrose solution. Number of pollen grains per anther per flower was determined by using the method suggested by Lloyd (1965). Number of ovules in the ovaries was counted by crushing the pistils on a glass slide in lacto phenol aniline blue. Pollination mode was determined by observing the trees in full bloom. Wind mode of pollination was confirmed by examining glycerine smeared glass slides for pollen, hung at different levels at all sides of the tree during peak flowering. For insect pollination, insect activity was examined at 1 hour intervals. The frequency, time and pattern of insect visitation were studied through visual observations. Insect visitors to floral heads were collected with a net, fixed in alcohol and identified. Self compatibility was determined through bagging unopened heads and examining the seed set. Seed maturation was used as an indicator of effective pollination and fertilization.

Table 1. Locations of sample trees of three varieties of *Acacia nilotica* in dry, semi-dry and sub-mountainous zones of North West India.

States	Zones	var. *typica* Locality	var. *kauria* Locality	var. *cupressiformis* Locality
Punjab	Dry	Bathinda, Faridkot, Ferozepur	Bathinda, Faridkot, Moga	–
	Semi-dry	Amritsar, Fatehgarh Sahib, Hoshiarpur, Ludhiana, Malerkotla, Patiala	Amritsar, Chhatbir, Hoshiarpur, Jalandhar, Ludhiana	Ballowal Saunkari
	Sub-mountainous	Anandpur Sahib, Garhshankar	Ghanaula, Ganguwal	Anandpur Sahib, Ganguwal, Jogewal, Mangewal, Mansewal
Haryana	Dry	Mandi Dabwali	–	–
	Semi-dry	Kurukshetra	Ambala, Pipli	–
	Sub-mountainous	Kalka, Panchkula	Pinjour, Surajpur	–
Uttar Pradesh	Sub-mountainous	Saharanpur	Saharanpur	–
Uttranchal	Semi-dry	Rampur, Roorkee,	–	–
	Sub-mountainous	Dehradun, Rishikesh	Haridwar, Rishikesh	–
Himachal Pradesh	Sub-mountainous	Naina Devi, Paonta Sahib, Una	Mandi, Naina Devi, Paonta Sahib	–
Rajasthan	Dry	Ganganagar, Hanumangarh, Kota, Raisingh Nagar	Hanumangarh, Kota	–

Wood quality as timber is estimated on the basis of moisture content (MC) %, specific gravity and weight density as per the method and formulae of Panshin and de Zeeuw (1980). Fuelwood quality is determined on the basis of calorific value using a Bomb Calorimeter (Adiabatic), and heat of combustion is calculated by using the following equation-

WT = HM, where

W = Water equivalent of bomb calorimeter

T = Rise in temperature

H = Heat of combustion of material in Cal. /g

M = Mass of sample in g

Fodder quality of leaves and pods was based on Crude proteins (CP), Neutral detergent fibers (NDF), Acid detergent fibers (ADF), Cellulose (C), Hemi cellulose (HC), Lignin, Ash contents and Tannins, as estimated per Vansoet's system of Analysis (1967). *In vitro* dry matter digestibility (IVDMD) is based on the *in sacco* technique of Tilley and Terry (1963). Gum yield has been estimated from the natural wounds/cracks and artificial incisions inflicted on the stem. Gum quality is determined on the basis of colour, with light coloured considered as of good quality. The bark tans from the boles and branches of young, mature and old aged trees were estimated every two months through the standard Indigo Carmine Titration Method (Anonymous 1957).

Results and Discussion

Acacia nilotica in North-West India exhibits morphogenetic diversity in the form of three varieties, namely var. *typica*, var. *kauria*, var. *cupressiformis*. The trees in each variety can be identified on the basis of crown, bole, spine, leaf and pod characters. The sample trees selected for germplasm evaluation and various aspects of flowering phenology, floral biology, pollination mechanism and breeding system were found to be sexual diploid (n=13) with normal meiotic course, high pollen fertility (more than 90%), and good pod and seed set.

A. Reproductive biology

Phenologically the species passes through a brief deciduous phase of 28–36 days during winters (January-February) and a long and staggered flowering period of 161–189 days with peak blooming during monsoon months of July-August. Flowering phenology phase is nearly the same in the three varieties except that the opening of floral buds is delayed by 15–20 days in var. *cupressiformis*. Wyatt (1982) opined that species with extended flowering phase would be at an advantage in term of probability of fruit set. Such a case can also be attributed to *A. nilotica* where fruit setting initiation is high (up to 26%) but a low percentage of fruit reach maturity (up to 4%). This seems to be the consequence of premature fruit fall at various stages of pod development owing to wind currents and pest attack of young fruits. The species bears pods biannually, first in October to December and for a second time during January to May. Pod set and maturation is lower for the first pod set, probably due to low temperature and frost conditions. Of the three varieties, trees of var. *typica* show relatively high pod set (3.4 ± 0.86% to 4.8 ± 0.98%) compared with the var. *kauria* (1.00 ± 0.79% to 2.00 ± 1.28%) whereas var. *cupressiformis* shows the lowest percentage fruit set (0.30 ± 0.20%). On provenance basis, trees growing in semi-dry zones show relatively high percentage of mature pods compared with dry and sub-mountainous zones. It has also been observed in this study that trees growing in populations and plantations bear higher number of fruits compared with the isolated individuals.

The small sized, tubular, and sessile flowers, with the odour of ripe lemon, are present in bright yellow globose and fluffy cymose heads, arranged in panicles. The heads are the largest in var. *cupressiformis* (1.38 ± 1.02 cm x 1.40 ± 1.00 cm), closely followed by var. *typica* (1.32 ± 1.10 cm x 1.38 ± 1.03 cm), whereas those of var. *kauria* are the smallest (1.25 ± 0.06 cm x 1.27 ± 0.09 cm). The size and number of flowers in a head is also the highest in var. *cupressiformis* (5.3 ± 3.0 mm x 3.5 ± 1.2 mm, 46 ± 2.14) and lowest in var. *kauria* (4.9 ± 0.8 mm x 2.0 ± 1.0 mm, 37 ± 2.70). Flowers in each variety are similar in structure. These are bisexual but a considerable number of these are functionally male due to the presence of a sterile pistil. The result, based on dissection of 1875 flowers from 50 heads (Table 2), depicted that frequency of such flowers ranges from 32.63% in var. *typica* to 49.25% in var. *kauria* and up to 57.00% in var. *cupressiformis*. The frequency of such flowers is relatively more in the basal position (69.95 to 88.25%) than those at the top (9.75 to 20.19%) and

Table 2. Data on number and position of flowers with sterile pistil in a head in three varieties of *A. nilotica*.

Variety	Total no. of heads dissected	Total no. of flowers dissected	Number & position of flowers in a head	% of flowers with missing carpel	Percentage of missing carpel (Total)	Percentage of functional carpel (Total)
typico	20	675	T=170 M=335 B=170	9.75 18.19 69.95	32.63	67.37
kourio	15	600	T=70 M=260 B=170	14.45 49.94 83.36	49.25	50.75
cupressiformis	15	600	T=140 M=320 B=140	20.19 62.56 88.25	57.00	43.00

T= 10 flowers in top position
M= Median flowers (remaining after T and B have been counted)
B= 10 flowers in basal position

middle (18.19 to 62.56%). Wyatt (1982) suggested that number of flowers and their arrangement in time and space determines the pollination level and fruit setting. Richard (1997) opined that aggregation of flowers in a head provide a greater reward per pollinator flight and a sufficient landing base for the insect pollinators, particularly the bees and butterflies that treat the head as one flower.

Flower structure is known to affect the pollination and breeding system of the species. Presence of small sized and tubular flowers in a head with long exserted stamens add to anemophilous pollination as has been reported earlier in *Plantago lagopus* (Sharma *et al.* 1990). However, the mass effect of flowers in bright yellow cymose heads with the odour of ripe lemon seems to play the role of a primary attractant for insect visitors, encouraging entemophily. A variety of insects visit the floral heads during peak blooming. Active pollination is achieved by the anther and/or pollen foraging bees (*Apis florea*, *A. mellifera*), wasps (*Polistes herbreus*) and butterflies (*Pieris brassicae*, *Danaus chryoppus*). The second mode of pollination involves rather passive contact by beetles (*Mylabrus purtulata*, *Meladora* sp.), black ants (*Solenopsis geminata*) and walkers (*Pyrilla perpusilla*). A small number (3) of Hymenopteran insects briefly visited the flowers during the study period but were not likely to be significant pollinators.

Apis bees are most active between 10.00–11.30 hr, which coincides with pollen availability i.e. the time of anther dehiscence (08.00–12.00 hr). The bees pay 16–24 visits and spend the maximum time of 24–30 s per visit. The wasps and a butterfly (*P. brassicae*) pay 8–11 and 6–7 visits respectively, and spend only 12–20 s per visit. Regarding the pollen load, honey bees and wasps carry 8–12 polyads, and a butterfly (*P. brassicae*) carries 4–6 on its body parts. Insects such as beetles, black ants and walkers act as minor pollinators carrying only few polyads. The arrangement of flowers in an inflorescence has a profound effect on the types of insects involved in pollen transfer. In *Acacia nilotica*, the opening of flowers is centrifugal and is suited to bees (mellitophily) and butterflies (psychophily) which move from the centre of the head towards the periphery.

Richards (1997) opines that opening of flowers and pollen presentation directly affect the pollinator flight patterns and hence pollination success in the species. In *A. nilotica*, 80–90% flowers in a head open during night (18.00–24.00 hr) and all the anthers in a flower dehisce synchronously the next morning between 8.00–12.00 hr. As a result the pollen is presented to the visiting insects *en masse* ensuring high pollination success. Furthermore, the considerable number of functionally male flowers (32.63–57.00%) serves to attract the pollinators and increase pollen flow in the population.

Pollen grains in the species are present in the form of 16-celled polyads which are of *Enterolobium*-type, with no significant variation in size in three varieties (48.07 ± 1.12 µm to 50.40 ± 1.08 µm). The individual pollen grains are small sized ranging from 11.92 ± 0.27 µm (var. *kauria*) to 12.26 ± 0.31 µm (var. *typica*). Apparent pollen

fertility is quite high (92.13 ± 3.44% to 97.89 ± 1.02%), and higher during peak blooming (Table 3). The pollen viability is low during the initiation (83.19 ± 2.81% to 93.42 ± 2.03%) and decline of flowering (70.00 ± 1.98% to 80.11 ± 1.01%). Actual pollen viability, as estimated through germination, ranges between 58% to 65%. Pollen viability decreases with storage from 43.75% to 3.12% and pollen fail to germinate beyond 7 days of storage. Pollen tube length also decreases from 120 µm to 9 µm in stored pollen grains.

The pollen grains are effectively transferred by the anther and pollen foraging bees, wasps and butterflies. Some pollen grains are also transferred through wind. However, actual examination of seventy two stigmatic styles reveals that only one or two polyads were present on these small sized stigmas. It has been observed that after half an hour of polyad transfer the stigmatic styles show watery secretion, which helps in adhesion and germination of individual pollen grains.

Pollen – Ovule (P/O) is another indicator of pollination and breeding system of the species. On the basis of P/O ratio (562.50–625.00), the species falls under the category of facultative out-crosser in spite of it being predominantly xenogamous. According to Cruden (1977), P/O ratio in the members of Asclepiadaceae and Mimosaceae are exceptions in the xenogamous group. In these families, pollen grains are grouped in pollinia or polyads, and the criteria for categorization of breeding system is not the P/O ratio but the ratio of pollen grains in a pollinium or polyad and the number of ovules per ovary. In *A. nilotica* this ratio is 1:1 (16 pollen per polyad and 16 ovules per ovary) indicating that the species has good pollination success owing to the excellent relationship between number of pollen and number of ovules.

Little work has been done on the level of self pollination and degree of self incompatibility in the species (Tybrik 1989). Mandal *et al.* (1994), on the basis of enzyme analysis, suggested the species was self compatible and that 60% of the seeds are set through self pollination. Present studies revealed that natural self pollination in a flower is avoided due to herkogamy as the stigma is at a higher level than the stamens. Selfing through geitonogamy is also not successful, because from 675 heads bagged containing approximately 27,000 flowers, only 11 pods were set. In spite of the fact that a considerable number of flowers in a head have a sterile pistil, trees in each variety produced a good number of pods and seeds per pod at least during the second phase of fruiting. Such reproductive success can be attributed to effective pollen transfer and an excellent correlation between number of pollen grains per polyad and number of ovules per ovary. Out of three varieties, var. *typica* showed better reproductive success with respect to seeds (27,472 ± 58) whereas var. *cupressiformis* showed relatively poor fruit bearing capacity and lesser number of seeds (9600 ± 28). This may probably be due to the fact that var. *typica* exists in populations and trees of var. *cupressiformis* as isolated individuals.

Table 3. Pollen fertility in different varieties of *A. nilotica* at different phases of blooming from dry, semi-dry and sub-mountainous zones of North West India.

Zone/s		Pollen Fertility (%)		
		Initiation of flowering	Peak blooming	Decline of flowering
typica	Dry	93.48	98.24	78.75
	Semi-dry	95.88	98.58	81.20
	Sub-mountainous	90.90	96.85	80.38
	Mean	93.42±2.03	97.89±0.74	80.11±1.01
kauria	Dry	84.35	94.15	77.94
	Semi-dry	88.76	96.37	78.11
	Sub-mountainous	85 .49	92.86	73.30
	Mean	86.20±1.86	94.46±1.44	76.45±1.52
cupressiformis	Sub-mountainous	83.19±2.81	92.13±1.69	70.00±1.98

B. Germplasm evaluation

The species in India is recognised as one of the best MPT species as a source of timber, fuelwood, fodder, gum, tannins and for other minor purposes. The three varieties show different values for different parameters of these economic attributes.

I. Wood quality

Previously, Pearson and Brown (1932), Rao and Purkayastha (1972), Kaushik *et al.*(1984), Tewari and Rajput (1987), Shukla *et al.* (1990) and Purkayastha (1996) studied the physical and mechanical properties of wood. In the present study wood quality was estimated both as timber and fuel wood.

(i) Timber: The timber quality was determined on the basis of MC%, specific gravity (green and OD) and weight density. MC% in the species ranged from 46.31% to 69.43%. Negi (2000) also noticed a wide range of MC% in the trees growing under the same locality in populations of Haryana. On variety basis, average MC% was highest in wood of var. *cupressiformis* (69.43 ± 2.04%) and lowest in var. *typica* (53.34 ± 7.10%). MC%, as high as 73.26 %, was recorded in some trees of var. *cupressiformis* growing in Hoshiarpur (Punjab). On the other hand, a relatively low MC% (44%) was recorded in some trees of var. *typica* from Hanumangarh (Rajasthan). On provenance basis, trees growing in sub-mountainous zones contained relatively high MC% (63.07 to 69.43 %) as compared to those growing in semi-dry (50.65 to 64.11 %) and dry regions (46.31 to 48.77 %).

The wood of var. *kaurio* had the highest specific gravity under green conditions (0.77 ± 0.04) compared with that of var. *typica* (0.69 ± 0.16). Specific gravity as high as 0.92 was recorded in the wood of some trees of var. *kaurio* growing in Hanumangarh (Rajasthan). However, some individuals of var. *cupressiformis* growing in Hoshiarpur (Punjab) showed very low specific gravity (0.49). Specific gravity of OD wood was highest in var. *typica* (1.09) and lowest in var. *cupressiformis* (0.80). The highest specific gravity of OD wood (1.31) was recorded in the wood samples of var. *typico* collected from the dry regions of Bathinda (Punjab) and Ganganagar (Rajasthan). Specific gravity as low as 0.69 was recorded in trees of var. *cupressiformis* from Ganguwal, Ropar (Punjab). On provenance basis, wood of trees growing in dry areas had a higher specific gravity compared to those growing under semi-dry and sub-mountainous zones.

On a weight density basis, wood of var. *typico* was the heaviest (1.39 ± 0.04 g/cc) compared with that of var. *kouria* (1.17± 0.01 g/cc) and var. *cupressiformis* (1.15 ± 0.01 g/cc).

On the basis of these parameters, trees of var. *typico* growing in dry and arid zones yield the best quality timber. Troup (1921) has also inferred that wood of var. *telia* (var. *typico*) has a better reputation than other varieties.

(ii) Fuelwood: The wood of *A. nilotica* provides good fuel due to high calorific value and excellent burning quality with gradual burning. Density of smoke during burning is very low, and moreover, it produces no sparking or cracking during burning (Dwivedi 1993). The heating power of wood of *A. nilotica* is very high ranging between 4236.55–4950.75 Kcal/Kg. Among the three varieties, var. *typica* yields the best fuelwood with highest calorific value (4875.91 Kcal/Kg ± 53.14) and var. *cupressiformis* (3900.25 ± 50.22) the lowest. On provenance basis, trees of dry zones provide better quality fuel wood than those of semi-dry and sub-mountainous zones.

II. Tannins

'Babul' bark is the most important bark used by the tanneries in Northern India because it is cheap and abundant, and is easily obtained as a by-product after the trees are felled for fuel or timber (Trotter 1940; Mehta 1981). Bark tans from bole ranges between 12 to 20% with old trees containing more tannins (Mehta 1981; Anonymous 1985; Dwivedi 1993). Present results also indicated that average tannin content was high and variable (17.80 to 38.07%) with some old aged trees of var. *typico* from semi-dry regions containing as high as 40.87%. Trees of var. *typica* contained the highest percentage in both bole (21.89 to 38.07%) and branches (9.81 to 12.34%). Whereas trees of var. *cupressiformis* had the minimum quantity of bark tans, 17.80 to 24.69% and 7.37 to 10.85% in boles and branches, respectively. The content of tannins in the bole (18.76 to 29.54%) and branches (8.75 to 11.00%) of mature (11–20 yrs old) trees was significantly higher compared with 5–10 yrs old young trees. The amount of bark tans also varied significantly in different geographical and

climatic regions where sample trees were growing. The bark tans in the bole and branches of all age group trees were much higher in trees growing in semi-dry regions compared with those of dry and sub-mountainous regions. On the basis of data collected at 2-month intervals, it was observed that quantity of bark tannins is highest during rainy months (July-August). The next best season for tans from bole is during winter months (January-February), whereas for branches tannins are the highest during March–April.

Thus, mature var. *typica* trees collected during April-May or January-February provided the best yield.

III. Gums

'*Babul*' gum exudes from natural wounds or cracks in the stem bark mainly during the hot and dry months of March-June. But the natural gum oozing process is slow, taking nearly a month or so. The average gum yield per year in trees of var. *typica, kauria* and *cupressiformis* was 17.33g ± 4.10, 11.67g ± 3.29 and 22.00 ± 6.16 g, respectively. However, it was observed that tapping through artificial incisions stimulated the gum flow, taking 5–7 days in dry, 10–12 days in semi-dry, and 18–22 days in sub-mountainous zones. The gum yield in the species can be enhanced from 3–17 times by inflicting incisions on the stem. It was also noticed that a blaze of 35x10 cm exuded the highest quantity. The freshening of these cuts at regular intervals with a solution of N/5-N/15 NaOH further enhanced the gum oozing process and yield, as has also been noted earlier by Dwivedi (1993) and Shiva *et al.* (1998).

The present study of three varieties revealed that gum yield also depended upon the age of tree, the area/provenance where the trees were growing, and size of incisions. The trees between the ages of 11–20 yrs gave the maximum yield. Beyond 20 yrs of age the gum yield reduced significantly. Very young (5–10 yrs) and very old trees (>40 yrs) produced only negligible quantity of gum as has also been reported earlier (Anonymous 1985; Dwivedi 1993). On variety basis, the average yield from natural wounds and artificial incisions was highest in var. *cupressiformis* and lowest in var. *kauria*. It was also observed that trees growing in dry regions yielded more gum compared with those of semi-dry and sub-mountainous zones. The colour of gum ranged from pale white to yellowish or dark reddish brown to almost black, depending upon the age of tree and presence of tannins in the bark. The young trees produced light shaded superior quality gum compared with the old aged trees. The trees of var. *typica* and var. *kauria* produced better quality gum with lighter colour whereas those of var. *cupressiformis* yielded poor quality gum with dark brown colour.

IV. Fodder

Acacia nilotica yields an excellent fodder both as leaf and pod, and trees are extensively lopped for the purpose (Singh 1982; Verma & Mishra 1989; Dwivedi 1992, 1993). The fodder quality of leaves and pods was determined on the basis of various constituents and IVDMD. The leaves contained relatively higher CP contents (18.50 to 20.15%) compared with pods (12.25 to 12.68%). Cellulose and hemicellulose were present in good quantity, with pods containing relatively higher cellulose contents (12.80 to 18.76%) compared with leaves (6.98 to 9.25%). However, the trend for hemicellulose is reversed, being much higher in leaves (12.00 to 18.05%) than pods (7.95 to 12.90%). At variety level, the cellulose in leaves was significantly higher in var. *typica* (9.28 ± 1.17%) compared with var. *cupressiformis* (6.98 ± 1.00%). But in pods, the amount of cellulose was higher in var. *cupressiformis* (18.76 ± 1.17%) compared with var. *kauria* (13.25 ± 0.42%) and var. *typica* (12.80 ± 0.97%). As far as hemicellulose is concerned, the amount in leaves was the highest in var. *kauria* (18.05 ± 2.54%), but in pods the hemicellulose was the highest in var. *cupressiformis* (12.90 ± 0.63%).

The lignins, which are known to affect the availability of cellulose and hemicellulose in fodder, were relatively low in leaves (5.50 to 6.60%) compared with pods (6.35 to 8.20%). The leaf lignins were higher in var. *kauria* (6.60 ± 1.12%) whereas for pods the amount was highest in var. *cupressiformis* (8.20 ± 0.89%).

Ash content was much higher in leaves (11.18 to 12.80 %) compared with pods (5.80 to 7.24 %). At variety level, var. *cuperessiformis* had the lowest ash content in leaves (11.18 ± 0.65%) and var. *typica* had the highest amount (12.80%). But for pods, the ash contents were the highest in var. *typica* (7.24 ± 0.76%) and lowest in var. *kauria* (5.80 ± 0.13%).

The NDF and ADF were much higher in pods compared with leaves. At variety level, the NDF and ADF

from leaves was significantly higher in var. *kauria* and lowest in var. *typica*.

Tannins, which are found to affect the fodder quality, were higher in pods (5.65 to 6.20%) compared with leaves (4.30 to 5.00%). The leaves of var. *typica* contained the lowest quantity of tannins compared with other varieties. Leaves of all three varieties showed higher IVDMD compared with pods. At variety level, leaves and pods of var. *typica* were the most digestible with 79.65% and 70.65% IVDMD, respectively.

Overall evaluation of germplasm for wood as timber and fuel wood, in three varieties from dry, semi-dry and sub-mountainous zones reveals that trees of var. *typica* growing in dry and arid zones of North West India provide the best quality wood both as timber and fuel wood owing to low MC%, high specific gravity and weight density, and high calorific value. On the other hand, var. *cupressiformis* yields poor quality wood due to high MC%, low specific gravity and weight density. The better quality of wood as timber and fuel wood in var. *typica* can be attributed to low vessel frequency, high fiber frequency and greater fiber wall thickness.

Among the various tanning materials used in tanneries in Northern India, bark tans of *A. nilotica* are the most important as these are usually obtained as a by- product after the trees are felled for timber or fuel wood. Of the three varieties, var. *typica* yields the minimum quantity of tannins, followed by var. *kauria*, whereas var. *cupressiformis* gave the maximum bark tans. On age basis, old age trees (>40 yrs) should be preferred for bark tans. Also it has been inferred that to get good yield, trees must be harvested for bark either during rainy (July-August) or winter months (December-January).

'Babul' gum is an important article of local importance and is used as a substitute of *'true gum arabic'*. The gum yield is the highest in var. *cupressiformis*, whereas var. *kauria* yields the lowest quantity. Trees growing in dry zones yield more gum compared with those of semi-dry and sub-mountainous zones. Gum yield can be enhanced up to 17 times by inflicting incisions of the size of 35 x 10 cm on the bole. Yield can be enhanced further if these cuts are freshened at regular intervals with N/5-N/10 NaOH. Trees of var. *typica* yield the higher quality, lighter coloured gum compared with that obtained from the trees of var. *cupressiformis*. It has been also observed that young aged trees in all the varieties yield lighter coloured gum. If quality is not under consideration and darker coloured gum serves the purpose (as an adhesive), even the old aged trees can be tapped.

On the basis of higher amount of CP, Cellulose, HC, and ash contents, and low amount of NDF, ADF, lignins and tannins, coupled with good IVDMD, *A.nilotica* yields the best fodder and is equivalent to *Grewia optiva* and *Morus alba*. Variety *typica* produces the best quality fodder whereas var. *kauria* gave the poorest quality fodder.

From the above account it has been inferred that for the majority of the parameters, var. *typica* is far superior to var. *kauria* and var. *cupressiformis*, and would be recommended as a preferred variety for plantations.

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A new combination in *Gentianella* for the Australian species *Chionogentias demissa*

a235999

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Note

Glenny (2004, p 518–519) made combinations in *Gentianella* for Australian species whose basionyms were in *Gentiana* or *Chionogentias*. Unfortunately one species was not included and a combination for this species is made here:

Gentianella demissa **(L.G.Adams) Glenny *comb. nov.***

Basionym: *Chionogentias demissa* L.G.Adams, *Austral. Syst. Bot.* 8, 960 (1995).

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